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ANIMAL ECOLOGY

With Especial Reference to Insects

BY

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To
MY FORMER GRADUATE STUDENTS
WHOSE INSPIRATION AND AID MADE
THIS VOLUME POSSIBLE

PREFACE

The subject matter of this volume had its origin in a course in Insect Ecology which was given at the University of Minnesota beginning in the year 1917. The course underwent a gradual evolution and was never given twice the same. In 1925 the lecture notes appeared in mimeographed form for the students. Since that time, the present manuscript has been in the process of preparation and continual revision. In some phases of the subject matter results of new researches have been appearing so rapidly that it has been difficult for the work of revision to keep up with the current literature. In 1930 it became evident that the manuscript must be closed even though it would necessitate the neglect of certain new publications.

The volume is now presented for publication in the hope that it may prove useful to students and research workers in the field of animal ecology. There is no feeling that the method of outlining the subject matter is necessarily superior to any other method or that the examples which have been chosen to illustrate the various principles are the most important ones to be found in literature. If the volume fulfills its purpose in aiding those engaged in ecological research it will soon become out of date.

In so far as possible the material presented has been quantitative. This is not so much because the descriptive observations of naturalists are less valuable, but rather because the quantitative results of experimental research lend themselves more readily to critical consideration.

During the course of the preparation of the manuscript, the author has been aided so much by colleagues at the University of Minnesota and in the various entomological laboratories in different parts of the United States and Europe that it is difficult to do justice in thanking them for their many kindnesses. All of the authors who are cited throughout the volume in connection with the materials furnished for tables and illustrations are due special thanks for their kind cooperation. Dr. Volterra gave permission to reprint his paper on the fluctuations of the numbers of animals as an appendix to this work, thus making it readily available to those interested in insect ecology.

Special thanks are due to Dr. W. A. Riley, Professor A. G. Ruggles, Drs. S. A. Graham, V. E. Shelford, E. Booker Klugh, and Chancey Juday.

The author also wishes to thank Mrs. Marie Spriestersbach, Misses Frieda Hinnenkamp and Lillian Baird, and Messrs. Ralph King and John Stanley for aid in the preparation of the manuscript and bibliography. The author, however, assumes full responsibility for the accuracy of the manuscript.

ROYAL N. CHAPMAN.

THE UNIVERSITY OF HAWAII, HONOLULU,
August, 1931.

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ANIMAL ECOLOGY

CHAPTER I

INTRODUCTION

Animal ecology, as conceived at present, is of relatively recent origin although there is much truth in the statement that ecology is nothing more than scientific natural history. Certain foundations for our present conceptions of ecology were laid in earlier years by naturalists, physiologists, zoogeographers, and biometricians.

Buffon (1707 to 1788) is pointed out by Lankester as the only prominent writer on natural history who could be accorded historic rank in the field of natural history during this early period. Buffon himself opposed the then orthodox study of the structure and classification of animals, and called attention to the "bionomics" or inter-relations of organisms. He popularized descriptions of his observations to a certain extent in 44 volumes published during six years while he was keeper of the royal garden.

Alexander von Humboldt (1764 to 1859), a botanist and explorer, laid certain foundations in the field of distribution of organisms in connection with descriptions of species and the factors of climate and geography affecting them.

Malthus (1772 to 1844) in his "Essay on the Principles of Population" (1806) laid foundations in biometrical work which have had a great influence in biology. This work served as an inspiration for Wallace, Darwin, and other biologists as well as investigators in the field of statistics.

Isidore Geoffroy Saint-Hilaire in his "Histoire générale des règnes organiques" (1859) stated in the introduction that the last volume of his work would be devoted to the subject of "ethology." Unfortunately, this volume of his work was never published and we have, therefore, only his statement in the introduction to the earlier volume as to what this subject matter would be. He defined ethology as follows: "The study of the relations of the organism within the family and the society, in the aggregate and in the community." The laws of ethology were said to relate to the instinct, habits, and in general to the "external manifestations of organisms." This announcement, by Saint-Hilaire, of his intention to publish a volume on ethology defined as above is taken by some authors to constitute priority over the term "ecology" which has

come into current use. It seems quite evident that Saint-Hilaire was defining the subject matter which we now consider that of ecology.

Haeckel (1869) used the term "Oekologie" and defined it as comprising the "relation of the animal to its organic as well as its inorganic environment, particularly its friendly or hostile relations to those animals or plants with which it comes in contact." He considered oekologie to include the general economy of the household of nature.

The present branch of biology which we designate as ecology has been synthesized from these various beginnings and has been augmented by numerous investigations such as those of Hensen (1887), Möbius (1877), and others, which demonstrated the possibility of quantitative methods and emphasized the conception of an ecological unit or biocoenose. It is this conception of a unit of association bound together by the interdependence of the organisms which formed the association which has lent a great impetus to the development of ecology.

The advance of plant ecology has been more rapid than that of animal ecology. This has been due largely to the fact that plants are sessile and lend themselves to study of local distribution more readily than do animals. Thus the distribution of plants and plant association over geographic areas, and the distribution of plant associations in a series of ecological succession has made much more rapid progress than has the study of animal associations. Warming's textbook on plant ecology did much to bring together and organize the material of plant ecology and stimulate further work.

The subject matter of animal ecology has been brought together to a certain extent by several authors. Adams' (1913) "Guide to the Study of Animal Ecology" has served as a source book of literature. Shelford's (1913) "Animal Communities" is essentially a description of the animal communities in the region of Chicago, Ill.; but it contains generalizations with regard to the subject matter of ecology in general, and pays particular reference to the organisms of various communities. Borradaile's (1923) "The Animal and Its Environment," gives an elementary treatment of animal ecology including general descriptive matter from natural history, and relatively little quantitative analysis of the environment. Other publications on the subject of animal ecology are widely scattered through the literature. Pearse (1926) published his volume on "Animal Ecology" which brings together a great deal of the material on the subject that is largely descriptive.

Elton's (1927) "Animal Ecology" has a dynamic viewpoint which is stimulating. It has aimed to present principles and has well-organized material. Some authors seem to wish to emphasize the complexity of nature without any attempt to show order. Elton has attempted to show that there may be order even in the most complex systems. He emphasizes the importance of the food chains in nature and the relative num-

bers of animals without setting up complicated systems of concepts and classification.

Shelford (1929) published his volume "Laboratory and Field Ecology." In the introduction of this volume he calls attention to the field of biocoenology, or the study of the associations of organisms, and emphasizes its importance. However, the volume in general is devoted very largely to the subject of autecology, and to the methods of analysis of environmental factors. In the second volume of Schröder's "Handbuch der Entomologie," dated 1929, the first chapter by Anton Handlirsch is entitled "Biologie (Ökologie-Ethologie)." This is devoted very largely to the life history of insects in relation to their physical and biotic environment.

The British Ecological Society of London began the publication of *Journal of Ecology* in 1913. This was originally and is still largely dominated by plant ecologists. The Ecological Society of America was founded in 1916 and began the publication of *Ecology* in 1920 as a quarterly journal in which original papers and reviews of significant literature are published. In the pages of this journal, animal ecology has been very well represented. The various abstract journals, and the various indexes to biological literature, are now classifying material under the heading of ecology and thereby aiding the ecologists in finding the significant literature which is so widely scattered throughout the publications on biology.

Publications on aquatic organisms furnish some of the best examples of the quantitative work. The purely descriptive work on the natural history of various animals is voluminous, and often contains observations which are interesting merely because they are curious. The popularization of such phases of ecology has attracted the attention of the public but has undoubtedly been a hindrance to the progress of ecology as a serious branch of science. Such work has not only tended to congest literature, but it has added descriptive detail to a subject which needs more than anything else to be cleared of details until it has been organized on the basis of verified facts supporting fundamental principles. After such organization has been brought about, many of the details which are now cited as being curious may be evaluated and tabulated in the scheme of things as being significant supporting evidence for the fundamental principles, or as mere coincidence of little scientific importance.

THE SUBJECT MATTER OF ANIMAL ECOLOGY

The subject matter of biology or the study of organisms may be divided on the basis of the biological phenomena which are studied into certain fundamental branches. We have thus: morphology, or the study of the structure of organisms; taxonomy, or the study of the phylogenetic groups of organisms and their relationship to each other; and physiology, or the study of functions of organisms. The inter-relations of organisms

in nature may be considered under the subject matter of ecology which is closely related to physiology, and in the minds of some biologists should be a subdivision of it. It has been said that ecology, when reduced to its lowest terms by a process of analysis, becomes physiology; that physiology, when reduced to its lowest terms by a process of analysis, becomes physiological chemistry; that physiological chemistry may in a similar way be resolved into biochemistry; biochemistry resolved into chemistry itself; and chemistry itself resolved into physical chemistry; and physical chemistry resolved into physics. However this may be, it is clear that an organism consisting of cells and organs is a physical structure combined in such a way as to produce a very complicated organism of cells and organs, and that these systems of cells and organs have certain characteristics as an organism. A thorough understanding of the physical structures which go to make up this system is of fundamental importance to physiology. Similarly the associations of organisms dealt with in ecology consist of organisms which, in turn, are these same physical systems. It is therefore essential that the ecologist have a thorough understanding of the principles of physics, chemistry, and physiology, in order that he may be familiar with the fundamental properties of the organisms which make up the associations with which he is to deal. For this reason it is necessary to incorporate into the subject matter of ecology much that is essentially physics, chemistry, and physiology. However, as will be pointed out in the course of the present volume, the behavior of systems of population is often dependent upon the characteristics of the organisms themselves as units. Their rates of reproduction, food requirements, etc., are characteristics of the organisms as such. Within the limits of the physical conditions of the environment which permit the normal functioning of the organisms, the reactions of the populations are dependent upon the characteristics of the organisms themselves and are relatively independent of the physical conditions, so long as they remain within the limits of the toleration of the organism.

The word "ecology" comes from the Greek root "oikos" meaning home. Literally ecology may be defined as a treatise of the home relations of organisms. This is essentially Haeckel's definition, which has already been given. Shelford (1913) gave the following definition: "Ecology is that branch of general physiology which deals with the organism as a whole, with its general life processes as distinguished from the more special physiology of the organs, and which also considers the organism with particular reference to its usual environment." In his more recent volume Shelford (1929) says that the third division of biological sciences is bioecology, which is the sociology of organisms. Further, he says,

At the present time there is no need and little justification for the term "autecology" as it has been interpreted relative to animals or for that matter for the

use of the term ecology referring to particular species as very commonly construed. Ecology is a science of communities. A study of the relations of a single species to the environment conceived without reference to communities and, in the end, unrelated to the natural phenomena of its habitat and community associates is not properly included in the field of ecology.

The subject matter of ecology was subdivided by Schröter into autecology (1896) and synecology (1902). Autecology is derived from the Greek root, "autos," meaning self; and synecology from the Greek prefix "syn," meaning together. A committee of which Schröter was a member made a report to the Third International Botanical Congress in 1910 (Article 8b) as follows: "The term 'ecology' comprises the whole of the relations existing between the individual plants or plant associations of one part of the station to the other part. (Ecology, the study of conditions of environment and of adaptation of plant species is if taken isolately 'autecology,' if taken in association 'synecology.'") On the basis of this definition we may therefore analyze the environment considering each of the physical and biotic factors which go to make it up separately as autecology. In so doing we may be applying the methods of physics, chemistry, and physiology, and it is difficult to see how we may properly appreciate the various factors unless we have so considered them. We may also study the species of organisms which go to make up the associations separately, and all this would be considered under the subject matter of autecology. When these physical factors are put together and considered as weather or climate making up the environment of organisms, and when we consider the various species of organisms in the natural associations in which they occur and study their interrelationships with each other and with the environment, we are then considering the subject matter of synecology. In the study of autecology it is quite evident that the work is bordering very closely on the field of physiology and might quite properly be considered as just an aspect of physiology. It is this aspect of autecology which has given rise to such statements as those of Shepardson (1929), that ecology is a viewpoint rather than a branch of science.

In turning to the subject matter of synecology and the treatment of the interactions of species on each other as a fluctuation of population, as is done in the Appendix by Dr. Volterra, we realize that we have come to a field which is no longer that of general physiology, but stands out more distinctly as that of ecology. Adams (1913) proposed the term "individual ecology," to represent the conception apparently identical with that of Schröter for autecology. Adams expressed this conception as the study of an individual or species either in a restricted environment or throughout its entire geographic range and including all its relationships to the complete environment. Since Schröter's term has priority and is more generally accepted, it seems best to adopt it. Adams also

proposed the term "associational ecology" for the study of the relationships of animals, groups, or those associated in the same habitats and environments. Again this term seems to be the same concept that is expressed in Schröter's synecology. Du Rietz (1921) presented a diagrammatic representation of various theories of the division of the subject matter of biology and in this included the term "idiobiology" for the same concept of the study of the individual organism.

Autecology will be interpreted as including the study of the various physical factors of the environment in relation to insects and other animals. It is true that this will be essentially physiology, but the viewpoint will be that of the factor as a part of the animal environment. This will be followed by a study of the individual characteristic of the organism and the two main headings will be "Physical Autecology" and "Biotic Autecology." In the consideration of biotic autecology it is very difficult to draw a distinct line between the so-called "autecology" and "synecology," for as soon as the biotic factors begin to operate upon an organism, we have the interaction of organisms which might be interpreted as being synecology.

Synecology will be considered as population systems on the basis of biotic potential and environmental resistance, and as distributional and descriptive ecology. The discussion of population systems is supplemented by the Appendix by Dr. Volterra. Distributional synecology will include the consideration of the distribution of the associations of animals in space as chorology or zoogeography, and their distribution in time as chronology or succession. Distributional synecology is thus dynamic. Under the chapters on descriptive synecology various types of environments will be considered. It is necessarily impossible to give an exhaustive study of any environment, or to list all the species that belong to the various associations.

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CHAPTER II

LIGHT AS AN ECOLOGICAL FACTOR

Life, as we know it on the earth, would be quite impossible if it were not for the receipt of radiant energy from the sun. It will not be necessary to dwell at length upon the general importance of solar radiation, a part of the energy of which is made available in heat for the earth and a part for chemical reactions. For the present, attention will be confined to the radiant energy which falls within the limits of human vision, and to the region of the solar spectrum lying on either side of this, which we ordinarily think of as light. The radiant energy which is characterized by the longer wave lengths will be considered under the topic of Temperature. From the standpoint of logic, we might well treat radiant energy as one subject, for it is often difficult to differentiate between heat and light. From the standpoint of practical pedagogical procedure, there are certain advantages in differentiating between these subjects.

Light may be defined as radiant energy within the limits of human vision. For our present purposes, we shall include all the shorter wave lengths of radiant energy up to and including the visible spectrum. We have thus included all the energy which is made use of by plants through photosynthesis and which is stored as coal, oil, and other natural resources of the earth directly or indirectly used by animals.

Before proceeding with the consideration of light as a factor in animal ecology, it is well to pause for a moment to consider light as such. There is possibly no conception more fundamental to physics than that of the nature of light; yet probably the most important current question in physics is the formulation of a conception of light which will be in full accord with all the facts which are now before us in regard to this form of energy. The student is referred to the most recent textbook in the field of physics and to the current literature in physics for a further consideration of this question, which involves almost our entire understanding of energy and matter as they exist in our universe. It is through light that we gain much of our information with regard to our physical environment. For our present consideration we shall look upon radiant energy as an endless procession of waves, each wave consisting of a mass of units or corpuscles, and the troughs between the waves as intervals in which these corpuscles are present in very small numbers. The frequency of the waves, or the distance from one wave to another, may be taken as a measure of the different characteristics of radiant energy.

A figure is presented (Fig. 1) which may aid in orienting the portion of radiant energy which we are considering as light, with respect to radiant energy in general. The first line at the top represents radiant energy up to a frequency of 20,000 meters. Most of this energy is that which is made use of in radio communication. On a scale as large as this, we can hardly perceive the area covered by what we are now considering as light. This is also true of the second line, which goes out for 40 meters; while the third line has been greatly magnified so that its

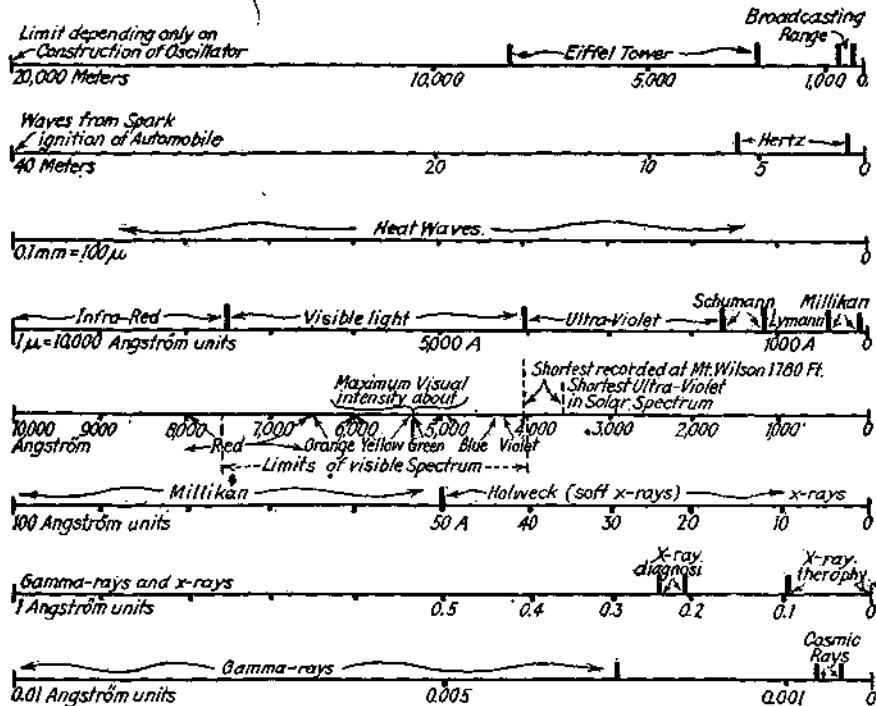


FIG. 1.—Diagram of wave lengths of radiant energy. Each line represents a scale of wave lengths ranging from meters on the top line to hundredths of an Angstrom unit on the bottom line. If the entire wave length included in the top line had been drawn on the scale of the bottom line it would extend from the earth to the nearest fixed star. (Taken from various sources; chiefly from Dr. John Tate.)

entire length goes out to a frequency of one-tenth of one millimeter. But even yet this line is occupied very largely by waves which we know as heat. The fourth line represents only one one-hundredth of the third line; and it is here for the first time that we are aware of the visible spectrum, which is shown more in detail in the fifth line. It is only that region which lies roughly between about 4,000 and 8,000 Angstrom units which is visible to us as light. There are shorter invisible rays which come to us from the sun, but the shortest of these are filtered out by the atmosphere of the earth as the rays approach us. Our maximum visual

intensity does not lie in the middle of the visible spectrum, but slightly to the short side. The greatest chemical or actinic effect is found in the shorter waves of the visible spectrum; while the longer waves are characterized by heat. The sixth, seventh, and eighth lines drawn in this diagram locate some of the various types of shorter rays. New investigations of these shorter wave lengths are coming forth every day with the perfection of the technique which will make observations possible. Investigation emphasizes the importance of these short rays, and the so-called "cosmic rays" seem to be very important in our conception of the balance of energies in our universe.

There are two important conceptions to be gained from this consideration of light. The first is that light as a physical factor is not a

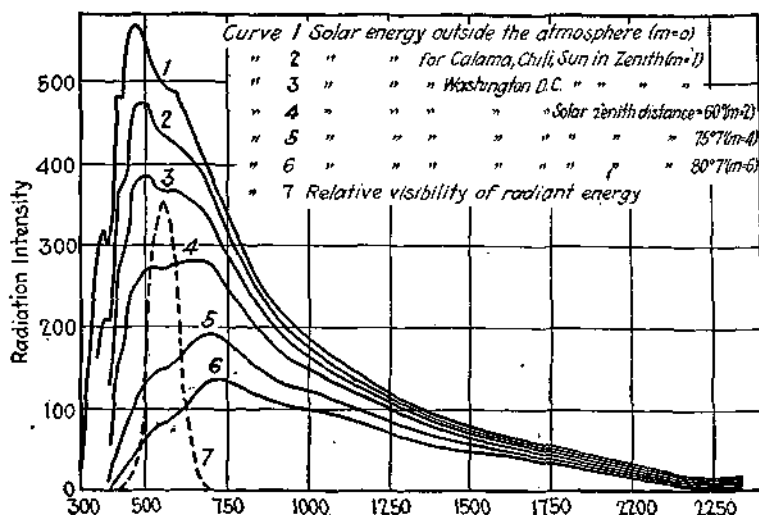


FIG. 2.—Normal solar radiant-energy curves, showing the distribution in the normal solar spectrum outside the atmosphere. Wave lengths are given in millimicrons; 1 millimicron = 10 Angström units. (Kimball, 1919.)

simple entity, but a group of radiations which we shall consider under one head for the purpose of convenience. The biologist who considers that his field is complex and that the field of physics is simple, will do well to consider what is involved in light including both the evidence as to the constitution of a single light wave and the great array of waves with all the characteristics belonging to their different lengths. If the diagram presented had all been drawn on the scale of the last line at the bottom, it would have extended from the earth to the nearest fixed star.

The second important consideration for the biologist is the fact that the field of physics, only a short time ago, considered its conception of light as almost a dogma. But it is at the present time engaged in the

process of reconstructing its conception of such a fundamental factor as light; and in this reconstruction, it has been necessary to cast aside many old and classical conceptions in order to bring theories into harmony with facts. Since this has been found necessary in the field of physics, biologists may expect finality on relatively few subjects during our present generation.

Methods of Measuring Light.—It is quite obvious from the consideration of the composition of light that it would be very difficult to make a measure, as to the quantity and quality of light, which would be equally applicable throughout the entire range. In the shorter wave lengths in our visible spectrum and the region immediately adjacent to it, we have a great chemical energy. In the longer wave lengths, we have heat involved. Any device which depends upon heat in making a measurement will measure the longer rays with relative accuracy, but the shorter rays with greater inaccuracy. Any device which depends upon chemical activity will measure the shorter rays with a greater accuracy, and the longer rays with less accuracy. Any device which depends upon brightness of light will measure, with any degree of accuracy, only that portion which lies near the center of the visible spectrum.

In an ecological investigation, it is necessary to measure not only the quality but the quantity of light present. This makes the problem doubly difficult. The types of instruments commonly in use for the measurement of light may be classed as: (1) pyrheliometers, (2) spectrographs and spectrometers, (3) photometers or actinometers, and (4) illuminometers. The first two, pyrheliometers and spectrometers, are the most satisfactory to the physicist, but are probably less practical for the ecologist.

A general consideration of the methods of measurement has been given by Klugh (1927).¹ Shelford (1929) gives a description of various methods of measuring light. The pyrheliometer is a standard instrument, the readings of which can be reduced to gram calories per square centimeter of surface. The principle depends upon the absorption of heat from the solar radiation. Various types have been made: the Smithsonian silver disc (Smithsonian Miscellaneous Collection, 1913), and other types made by Marvin, Kimball (1919), Angström (1919), and the more recent one by Gorczyński (1924). In this instrument a thermopile is mounted in a clock movement to follow the path of the sun. A Richard recording millivoltmeter is connected to record the thermo-electric current on a strip of paper. Since it is considered that

¹ This paper gives the results of comparative readings taken by the Moll-Richard-Gorczyński pyrheliometer, the MacBeth illuminometer, the Nutting polarization spectrometer, the Heyde aktinophotometer, the Drew justophot, the Wynne exposure meter and the neutral wedge with rhodamine "B" paper. The Canadian Research Council sponsored the experiments to obtain direct comparisons of these instruments for ecological investigations.

the thermo-electric current generated by the thermopyle, when exposed to the sun's rays, is proportional to the radiation intensity, it is possible to convert the reading directly into gram calories per square centimeter per minute of time. By the use of various color filters intercepted between the sun and the thermopyle, it is possible to study the intensity of the various qualities of light. In so doing, however, one is, in the last analysis, measuring the heat of the various light rays, and not the actinic properties of these rays.

Buxton (1926) devised a radiation integrator, which consists of a glass bulb welded within a vacuum sphere through which the light shines on the bulb. The latter is blackened in order that it may absorb the heat from the sun's rays. A tube extends from the bulb out through the sphere and down into a shelter, which protects it from the sun's rays. A certain quantity of alcohol is contained in the black bulb. The sun's rays evaporate the alcohol, which is then condensed in the tube, since it is shielded from the sun's rays and therefore cooler. The tube into which the alcohol is condensed, is calibrated to read in cubic centimeters. The readings are taken at intervals not longer than one day, and the readings of the quantity of alcohol which has been condensed are used as a measure of the amount of radiation during the period. The instrument has been standardized against Gorczyński's pyrliometer, and the readings converted into calories. Buxton believes this method to be preferable to that of a black and white bulb thermometer, similar to that used by Graham (1920). In the latter case two thermometers, standardized against each other, are mounted side by side in a box which protects them from the wind. One bulb is blackened; the other one, painted white; and the difference between the two thermometers is read off in degrees. The maximum difference for any given period is taken as 100 per cent of light.

Carter (1930) compared the readings which he obtained from a black and white bulb atmometer with the readings from a Kimball pyrliometer, and concluded that the readings as given by the black and white atmometer cups were essentially like those of the Kimball recorder. All of the pyrliometer methods are alike, in that they depend upon the heat of the sun's radiation. And it is possible in many cases that the ecologist will be interested not in the heat but in the actinic effect of the sun's radiation.

Spectrographs and Spectrometers.—From the standpoint of a study of the quality of light, nothing can be more satisfactory than a spectrograph. However, this instrument is cumbersome and difficult to use in the field. Furthermore, if quantity of light is to be measured, it is necessary to make a long series of exposures comparing the long exposures with the short ones in order to arrive at even a rough quantitative measure. It would seem that a field spectrograph which could make a

series of comparative readings for quantitative measurement would be of great advantage to the ecologist.

Photometers or actinometers depend upon the chemical reaction caused by the sun's radiation on an emulsion on a paper, film or glass plate. The range of sensitivity depends very largely upon the emulsion which is on the plate. The quantitative measurements made by the earlier photometers (Clements, 1905) were limited almost entirely to comparative measures.

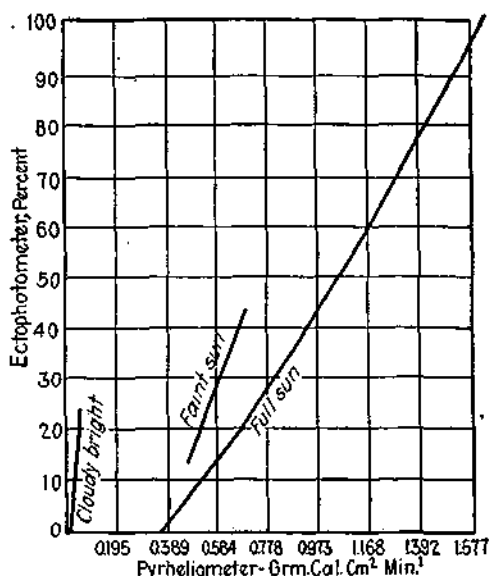


FIG. 3.—Comparison in total light energy, of the ectophotometer with a Moll-Richards-Gorczynski pyrheliometer. The graphs represent comparisons at different light intensities; from left to right, cloudy bright, faint sun, and full sunlight. (Klugh, 1927.)

The ectophotometer of Klugh (1925 and 1927) employs a set of standard color filters and the use of rhodamine "B" paper.¹ Klugh has calibrated this instrument so that it may also be read in terms of total light energy in gram calories per square centimeter per minute of time. This instrument, therefore, is able to read both quality and quantity of light and is sensitive enough to be read even at night in starlight and moonlight. When the total light energy in full sunlight, as read by the ectophotometer, is compared with the readings of the Moll-Richard-Gorczyński pyrheliometer, there is practically a straight-line relationship; but in faint sun or in cloudy bright light, the relationship is not a straight-line one, on account of the greater sensitivity of the ectophotometer as

¹ Rhodamine is one of the triphenylmethane papers and Klugh (1927) gives instructions for making and standardizing it.

compared with the pyrheliometer. This instrument, the ectophotometer, may be used for various purposes on land; or the aquatic model, in water.

A simpler type of photometer, which consists of the use of neutral wedges with rhodamine "B" paper, is described by Klugh (1927). He used various wedges obtained from the Eastman Company, with gradations from one to one-half, one to one-tenth, one to one-hundredth, and one to one-thousandth. The one to one-hundredth wedge proved the most satisfactory. It was mounted in a frame, which made it possible to make exposures 30 seconds or longer. The most satisfactory method of reading the results was found to be the use of a standard tint, which was prepared by exposing the paper to full sunlight with the value of 1.61 gram calories per square centimeter per minute. A standard tint was then made up to match this color. For the satisfactory use of such

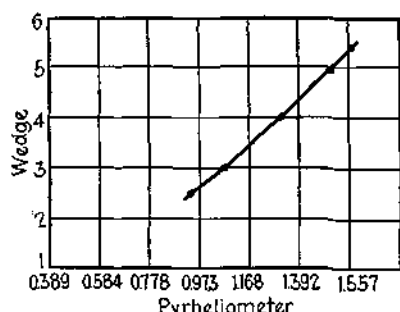


FIG. 4.—Comparison of the neutral wedge and rhodamine "B" paper with the Moll-Richards-Gorezynski pyrheliometer. (Klugh, 1927.)

an instrument, it is necessary to establish a scale of equivalence between the lighter and the darker tints which may be found under the various portions of the neutral wedge.

A similar photometer has been used in the laboratory at the University of Minnesota, in which a Goldberg wedge was mounted in a pocketkodak box with a shutter, which made it possible to make exposures of different lengths of time. Printing-out paper was mounted under the Goldberg wedge, and exposures, made for different periods of time. Readings were then made by comparing the times of exposure with the tint on the printing-out paper. Since the wedge is calibrated for a per cent of light transmitted, it is possible to find a point on the wedge at which the change in tint of the paper is fairly discernible. This serves for a comparison of light intensities between the two environments. By taking a series of exposures on a strip of paper, it is possible to draw a line connecting the various portions which show the slightest change in tint. By comparing the percentage of light required to make a change in tint in the paper, a comparison of the light in the environment is made.

Shelford and Kunz (1929) and Shelford (1929) describe the use of various types of photo-electric cells for the measurement of light. These may be used either for direct reading or for recording through the use of a potentiometer recorder. Shelford believes that the photo-electric cell offers the best possibility for measuring intensity (quantity) and quality of light. The present limitation to this method seems to be in getting cells which are standardized. The principle depends upon the

emitting of electrons by a metal when exposed to light. The variations in the cells are nearly as great as the variations in the light. The day will probably come when cells will be dependable enough for accurate work such as is required in ecology. The photo-electric cell has the limitation of not reading the red end of the spectrum.

Illuminometers have the advantage of giving a reading in foot-candle power. There are several types of field instruments which are made and which can be used to good advantage. They, in the end, depend upon the ability of the reader to compare a standard light with the light reflected from a disc exposed to the sun, or the light of the environment.

For a further consideration of the measurements of light from the standpoint of an ecologist, the student is referred to the papers by Klugh (1927) and Shelford (1929).

Methods of Controlling Light.—Light is the subject of a great deal of investigation at the present time from the standpoint of both physics and biology. One of the difficulties which has been confronted is that of controlling light for experimental purposes. Biologists, including entomologists, have usually considered it necessary to carry on all experiments in hothouses in order that the organisms might be exposed to what is called "normal sunlight." We now know that the glass of these houses intercepts what little ultraviolet light has been able to filter through the atmosphere of the earth. Consequently, the light in these houses is not normal. At the present time, we have glass on the market which is supposedly transparent to ultraviolet light, although there is some question as to how rapidly this glass will age and become opaque to ultraviolet light. Artificial light has been used as a substitute for daylight for many years. It has been used chiefly to lengthen the day during the period of the year when natural daylight is limited in time. The flaming carbon arc is one of the most satisfactory from the standpoint of spectrum, but it requires a great deal of care, needing almost continual attention.

Harvey (1922) and others have grown plants from seed to fruit entirely by the use of artificial light, no sunlight being involved at all. The nitrogen-filled tungsten filament (Mazda) lamp, mounted in reflectors, is used in most cases. The spectrum is quite similar to that of natural sunlight with the exception of some of the blues and violets. These bulbs require little attention, and the quantity of light can be varied either by distance or by the size of the bulb used. Automatic switches can easily be arranged for turning the lights on and off at any desired time. In experimental work with insects, the primary consideration seems to be to maintain the host plant under normal conditions. The primary requirement seems, therefore, to be that of plant physiology, and the literature on this subject is constantly growing and needs con-

tinual attention. Shelford (1929) discusses the general subject of the control of light for experimental purposes.

LIGHT AS A FACTOR IN ANIMAL ECOLOGY

Attention has already been called to the broad, general significance of light in all life. There are few living things which we can conceive of as existing on our earth without the presence of sunlight; even those that are at present adapted for living in darkness depend for their food and ultimate source of energy upon some forms which are directly dependent upon sunlight. It is the greatest single source of energy for biotic systems. It will not be necessary to dwell at length upon this general biological consideration. An appreciation of the importance of chlorophyll as a mechanism of photosynthesis and thereby the basic source of energy used by biotic systems will be taken for granted. Attention will be turned to the animal organism, especially the insect, as a mechanism which is affected in various ways in its energy transformation by the presence of light. In addition to that, insects in general have special organs for the perception of light, so that they may be guided in their activities in searching for food and avoiding enemies.

★ **Effects of Light on Physical and Chemical Processes.**—Every organism consists of a physical structure which accommodates the biotic system. It is, therefore, of fundamental importance to examine the effect of light upon the mechanism of this physical structure, before proceeding to other phenomena which may be classed as affecting the biotic system of the organism. In the consideration of the characteristics of the various parts of the spectrum of light, it has been pointed out that the shorter wave lengths are characterized by their chemical activity. We may, therefore, expect these short waves to have a great effect upon the physical mechanism of the organism. It is probably a generally recognized fact that light must be absorbed in order to have an effect.

A study of the effect of light and the physical processes which underlie the animal mechanism is attracting very wide attention at the present time. A detailed consideration of these new discoveries lies in the field of general physiology and will not be gone into in detail at this time. We may cite as an example Tröndle's demonstration (1910) that a weak light reduces the permeability of the cell membrane, a moderate light increases it, and a strong light diminishes it. Here, then, is a process of fundamental physiological importance which has an optimum light intensity. Either increasing or decreasing the light changes its functioning. Similar conditions are repeated over and over in the physical systems of nature, and therefore may be looked upon as of fundamental importance to all biotic systems.

Effects of Light on Biological Processes.—Biological journals are crowded with new contributions on the effect of light upon animals and

plants. The tendency of modern research is to study certain wave lengths of the spectrum. Consequently, most of the current papers are on the effect of various rays of light, but as yet the entire subject has not been summarized and the work evaluated in a comprehensive publication.

Much of the earlier work was done mainly to compare sunlight with darkness. Thus, Yung (1878) performed some crude experiments, in which he placed one lot of frogs' eggs in a dish in front of a window, where they never received the direct rays of the sun. Another he kept constantly in the dark. Under these conditions, which presumably were identical except for the presence or absence of light, the tadpoles in the light grew faster than those in the darkness. Davenport (1908) summarized the earlier work which had been done on organisms in general, and Bachmetjew (1907) gave a summary of work on insects. Some of the work up to this time was at least roughly quantitative. Belcard (1858) is classically quoted for his study of the effect of light on the flesh fly, *Musca*, under various colors of light, in which he found that the size varied; giving the largest under violet; the next under blue, red, white; and under green the smallest. It is stated that the larvae which developed under the violet light were three times the length and thickness of those under the green light. Gal (1898) reared the silkworm, *Bombyx mori*, under different lights, and noticed that the growth was different. The adult females laid more eggs and the cocoons were of larger size under green light. Next in order, so far as size of cocoons was concerned, came yellow, red, blue, white, and violet. The number of eggs from the female, however, did not follow this same order. It will be noticed that neither the order of size given by Gal nor that given by Belcard follows any particular system so far as the length of rays of the various lights is concerned. There may be some question, therefore, as to the significance of these earlier experiments. The nature of the evidence probably does not warrant general conclusions at the present time.

With all respect to the earlier literature, it may be of more advantage to turn attention to the later and more critical papers on the effect of light on biological processes. Davey (1919) studied the effect of x -ray upon mass cultures of *Tribolium*, and found that it was possible to prolong the life of a mass culture with a small daily dosage of x -ray. When the dosage was increased, the death rate approached that of the normal culture; but when it was increased still more, the culture died very quickly. Figure 5 shows graphically the general results of Davey's experiment. It is interesting to note that the time required for 50 per cent of the culture to die was 40 days in the control, and was prolonged to as much as 75 days in the experiments with about the optimum dose of x -ray. In these experiments, precautions were taken to see that x -ray was the only factor varying. It is not contended that x -rays are always

present as a normal part of light in nature. It is quite likely, however, that by a study of the effect of some of these special rays, we may gain some fundamental information with regard to the action of light rays in general. If the time comes when all of the rays have been studied in detail, we may be able to correlate the information on all of these rays

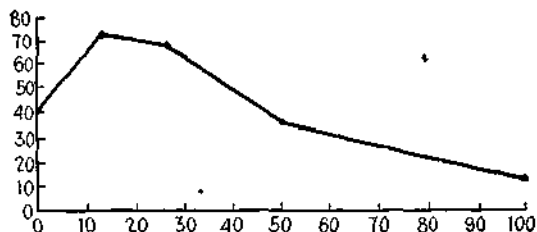


FIG. 5.—Graph showing the time required for 50 per cent of a *Tribolium* culture to die, plotted against the daily dosage of x-ray to which they were exposed. (Constructed from data taken from Davey, 1919.)

and form a general idea as to the physiological effect of light as such on organisms.

Packard (1926) made a study of the effect of x-rays upon *Drosophila* eggs for the purpose of determining whether or not they would be suitable material for measuring the quantitative biological effect of x-rays. This author did not find a stimulating effect of the low dosage of x-ray, but concluded that the Bunsen-Roscoe law of light intensity and time applied

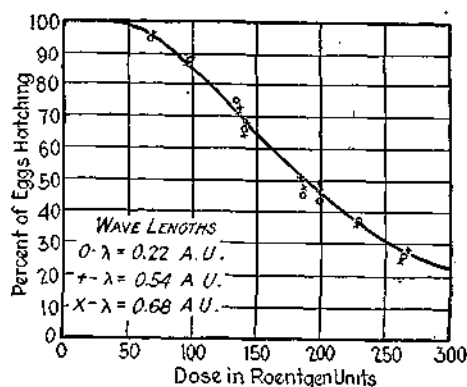


FIG. 6.—The relation between the dosage in Roentgen units and the death rate of *Drosophila* eggs. (Packard, 1927.)

here. This would mean that a shorter time at high intensity and a longer time at low intensity would give equal effects. In summarizing some of his experiments, he concludes that the mortality curves for *Drosophila* eggs have the same characteristics regardless of the dosage, but that the steepness of the curves varied with the intensity of the x-rays. Packard (1927) concluded that homogeneous x-rays of equal intensity but different wave lengths, varying from 0.22 to 0.68 Angström units,

produced the same quantitative biological effect on *Drosophila* eggs, and he found this to be true also for heterogeneous beams of equal intensity. Figure 6 is of interest because it seems to indicate that within the region of 0.22 to 0.68 Angström units, which covers in general the field of soft x-rays, there is not a great deal of difference in the quality of the rays themselves.

In further experiments, Packard found that by varying the distance in such a way that two beams of different wave lengths would give the same intensity, the effects for any given intensity were the same, even though one of the rays was in the region of soft x-rays and the other in the region classified as hard x-rays. The particular point of interest here is that these experiments seem to indicate that the nature of the

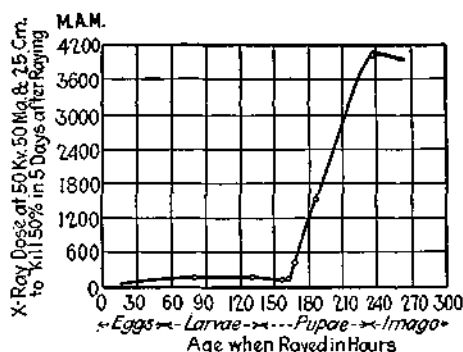


FIG. 7.—Graph showing the variation in susceptibility to x-rays with age in *Drosophila melanogaster*. (Mavor, 1927.)

effect is the same over a considerable range of wave lengths, when intensity as measured in Roentgen units¹ remains the same.

Mavor (1927) made a study of the susceptibility of *Drosophila* to x-rays in various parts of its life cycle. The graph in Fig. 7 shows the general results which were obtained. The eggs and larvae seem to have about the same amount of resistance, but during the pupal stage a very surprising change takes place. About 20 hours after pupation the resistance of the flies begins to increase, and at the end of pupation the resistance of the animals is about 35 times that at the beginning of the period. Mavor suggests that resistance begins to develop when the imaginal organs have been developed, and that this increases during the growth and differentiation of these organs. With regard to the effect of x-ray upon the rate of development, Mavor states that there is no evidence of any pronounced retardation, because of the exposure to x-ray.

¹ A Roentgen unit (German system) is that amount of x-rays which will produce, in 1 c.c. air at 760 mm. pressure and 20°C., an ionization current of one electrostatic unit.

Packard (1915) investigated the effect of some of the shorter rays upon *Drosophila*. The gamma and beta rays of radium were used, and the author concluded that the eggs and larvae of *Drosophila* are not appreciably affected by gamma rays. The rates of growth are apparently not changed at all, and the adults which emerge from larvae reared under conditions in which they were exposed to gamma rays are fertile. With regard to the beta rays, it is stated that larvae and pupae show no external changes even after an hour's exposure to a high intensity of beta rays. When the adults emerge, they are at first sterile, but soon become fertile. This seems to suggest that the oocytes may have been affected by the beta rays, and that the eggs which are later produced have been developed since exposure to the beta rays.

As a result of the work which has already been done on the effect of the short waves of light, it is perfectly clear that these rays may have a very great effect, also that the effect may vary from one insect to another, and during the different stages of the life history of any individual insect. Since this is the case, it is not going to be possible to make broad generalizations until a large amount of experimental work has been done and reported upon.

Work on higher animals suggests many other important effects upon the rates of biological processes. Data are rapidly being accumulated with regard to the effect of ultraviolet light upon vitamin D in the food of animals. Some preliminary unpublished experiments in this laboratory indicate that certain insects may be affected indirectly by food which has been irradiated with ultraviolet light. These will be referred to later in the chapter on Nutrition.

The effects of the longer rays of light upon the rates of the biological processes of insects have received less critical attention than those of the shorter rays. It has been the usual assumption that the ultraviolet portion of the rays of sunlight are necessary for the metabolism of insects. A search of the results of careful experimental work seems, at the present time, to lead to the conclusion that if the light conditions are sufficient for the host plant to grow normally, the insects will grow normally, and that those which do not require living host plants do not require light. Parker (1930) grew grasshoppers under artificial light and supplied the food daily. Under these conditions no alteration of rate of biological processes was noticed as compared with those which were reared in daylight. Wadley (unpublished thesis) reared aphids upon plants under artificial light conditions, and concluded that their growth was normal so long as the plants were normal. Northrop (1926) published the results of some experiments in which he ran mass cultures of *Drosophila* at a constant temperature of 25°C., one series being exposed to light and another being kept in darkness for 230 generations. Food was very carefully controlled in this case, both series receiving sterile

yeast as food. Since the lengths of the larval, pupal, and adult life were practically the same in both series, the author concluded that there was no evidence to show that inbreeding, absence of light, or growth in the absence of bacteria had any effect either on the duration of life or on the ability of the organisms to resist unfavorable bacteria. In the laboratory at the University of Minnesota, the author has reared *Tribolium confusum* during a period of 12 years in the absence of sunlight. Many of the cultures have been reared in continual darkness, and others at most have been exposed to the ordinary electric light used for laboratory observation. There is no evidence that the absence of light has made any difference whatever in the periods of the various stages of the life history, or in any other perceptible way.

It is known that certain insects, particularly those feeding upon green host plants, are affected by the length of day and, therefore, by light.

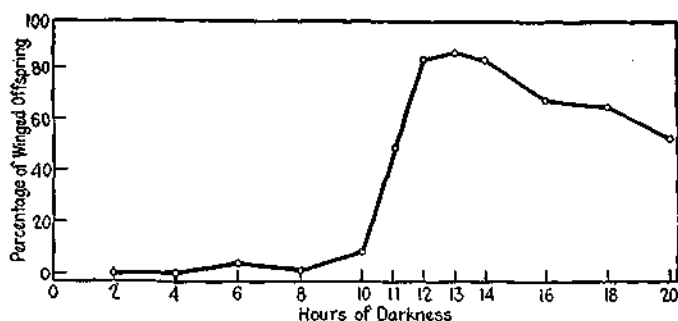


FIG. 8.—Curve showing the effect upon wing production of alternating the aphids between six hours of light and various periods of darkness. (Shull, 1929.)

Kellerman (1926) has given a summary of work on photoperiodism in plants and has summarized the important literature, showing that plants are definitely affected by the length of day. This is an interesting ecological factor because, leaving aside cloudiness, the length of daylight is definitely fixed by the angle of incidence of the sun's rays at various times of the year. Marcovitch (1923), Shull (1927, 1929a and 1929b), and others have given attention to the effect of photoperiodism on the production of winged individuals among the aphids. However, aphids are such highly complex organisms that it is not easy to experiment with them and make certain as to the quantitative effect of various factors affecting their lives with their varying sex ratio, their winged and wingless forms, and their peculiar method of reproduction. Shull (1927) found that *Macrosiphum* produces more winged individuals if reared under alternating light and darkness, than if reared in continual light. Continual darkness gives about as few winged individuals as continual light. Further investigation (Shull, 1929a) has shown a sharp increase of wing production to be correlated with an increase of darkness from

10 to 12 hours; a maximum effect with 12 to 14 hours of darkness; and a gradual decline in wing production for longer periods of darkness. The effect of the alternating light and darkness is apparently upon the parent, or upon the young before they are born. Starvation in darkness did not increase the number of winged individuals, but starvation in eight hours of light alternating with 16 hours of darkness gave the maximum number. It seems evident in this case, therefore, that it is a case of photoperiodism rather than the effect of light as such, for the rearing in continual light gives about the same results as rearing in continual darkness. Temperature is important as affecting the production of wings in alternating light and darkness. At temperatures higher than 20°C. few winged individuals are produced under any conditions of light and darkness, while the maximum effect is secured at lower tem-

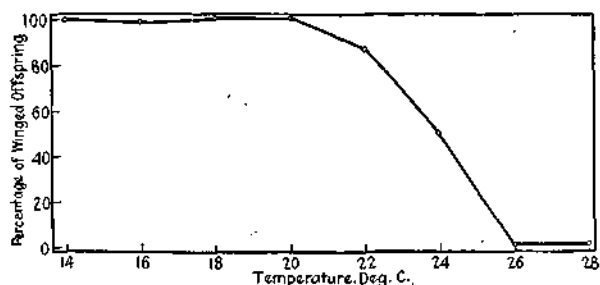


FIG. 9.—Curve showing the inhibiting effect of high temperature on wing production by alternating light and darkness, alternation of 8 hours light with 16 hours of darkness produces wings in almost all the offspring at all feasible temperatures up to 20°C., but rapidly loses this effect at higher temperatures. (Shull, 1929.)

peratures (Shull, 1929a). In nature these aphids develop winged individuals in the fall, when food becomes scarce, and days become short. This is important in their ecology; for they must migrate to another host at this time and, in the absence of wings, they would be powerless to do so.

The conclusions which may be drawn at the present time on the general subject of the effect of light upon the rate of metabolism of insects cannot be put in the form of broad generalizations, because of the lack of information. It is, however, encouraging to note that at least in certain cases light is not an important direct factor. Such insects as *Drosophila* and *Tribolium* apparently may continue to be reared under artificial-light conditions for experimental work, and it does not need to be considered that the experiments are at fault because natural sunlight is not being used. This is a great advantage, because there is hardly another ecological factor so difficult to control and experiment with as light; and if we may leave it out during the investigation of other factors, it will be an enormous advantage.

Effects of Light on Color, Form, and Structure.—In considering the effect of light upon the color of insects and attempting to evaluate the voluminous literature upon the subject, it is necessary to keep in mind the fact that there are several possible ways in which light may act upon color. For the present, attention is to be called to the effect of light, during the development of an individual organism, upon its color. This may come about either through the effect of light upon the development of the pigment in a fixed pattern, or, as is the case in other groups of animals, by stimulating the organism to rearrange its pigment to produce a pattern which the individual may change from time to time.

Poulton (1890) gave a summary of color of animals up to that date. Bachmetjew (1907) gave a summary of literature upon color of insects affected by light. Poulton cites experiments in which the larvae of certain butterflies, probably *Vanessa*, were reared on light and dark backgrounds and the chrysalis colored accordingly; those from light backgrounds became light colored, and those from dark backgrounds, dark colored.

Katheriner (1900) reports experiments on *Vanessa* in which the larvae were reared under various light conditions. Those exposed to daylight on a white background gave very light pupae; those exposed to daylight on a black background or to blue light gave dark pupae. In red light or yellow light the pupae were orange or yellow. Poulton considered that these effects were those of light upon the development of pigment; and this, in a way, formed the basis for his work upon protective coloration and mimicry. Standfuss (1894-1895) and others have carried on a series of experiments in which they have noted the effect of light upon the larvae as expressed in the adult which emerged. Hase (1929) reported the action of ultraviolet rays in inhibiting the formation of pigment in certain parasite wasps.

In much of this experimental work, due care was not taken to distinguish between the effects of low temperature and darkness. It is, therefore, difficult to evaluate these results. It seems, however, quite definite that light has a very important rôle in influencing pigmentation, and that certain organisms under certain conditions are light colored on light backgrounds, and dark colored on dark backgrounds. Folsom (1922) states that certain authors have considered this ability of insects to develop a light pigment on a light background and a dark pigment on a dark background as permanent protective coloration which may be regarded as stereotyped and the highly specialized end-stage of a more ancient ability to change color in response to color changes in the environment. The ability of certain crustaceans, fish, amphibians and reptiles to change their color in response to changing environment is well known. Some of the lizards are particularly adept in making quick changes from one color to another in response to the changed color of the environment.

Folsom quotes Wheeler as stating that this ability still exists in the case of some grasshoppers and mantids.

Perkins (1928) investigated the case of the shrimp (*Palamonetes*), in which the chromatophors expand or contract when the shrimps are placed upon backgrounds of different color, the chromatophors being expanded on black backgrounds and contracted on light backgrounds. In this case the photoreceptors are apparently in the eyes; for when the eyes are removed, the chromatophors are continually expanded.

Biedermann (1892) investigated the case of tree frogs and found that the migration of the pigment in the chromatophors was governed by receptors located in the toes, and that when these were anesthetized the frogs were no longer able to change their chromatophors to match the surroundings.

All of these reactions may be interpreted as methods used by the organisms to conceal themselves. In the cases just cited the individual organism can change its color from time to time to match its immediate surroundings. In the case of insects cited previously, where the pigment develops to a light color on a light background and a dark color on a dark background, there can be no change after the pigment is once developed. In the case of the chrysalis of lepidoptera, which are permanently attached, there is no occasion to change the color unless the background should change.

Modern experimental work seems to be becoming increasingly critical of such interpretations. It is admitted that there may be a process of selection in which the conspicuous animals are destroyed and the less conspicuous remain, but the usefulness of the adaptation seems to be in question. It would seem that the general proposition, when considered by and large, would have to be accepted, that the development of protective colors is of value to the organism. Physiological experiments are hardly to the point in determining whether or not these protective colors are valuable. When experiments have been performed to show whether or not members of a population which do or do not have protective coloration survive or are eliminated, we will have information which is to the point.

The effect of light upon the structure of organisms in general is a subject hardly well enough developed to be discussed to advantage. We know in general that animals which live in the absence of light have certain characteristics. Cave animals are classically quoted as being light colored and blind. Biologists of today find themselves in an embarrassing situation when considering such cases. We have, on the one hand, the seemingly overwhelming evidence of general evolution, into which the cases of blind animals in caves seem to fit very nicely. We have, on the other hand, the skeptical attitude of genetical research, which denies the possibility of the inheritance of acquired characters,

which seems to be implied in all interpretation of the structure of organisms which have lived in the darkness for generations. Consideration of this question leads us rather naturally to the next minor subheading.

The Effects of Light on the Mechanism of Heredity.—The development of our modern field of genetics with the allocation of various factors in genes that can quite definitely be assigned to places on different chromosomes, seemed at first to shut out all possibility of environmental influence in determining the hereditary characteristics of organisms. It seemed for a time that an organism was predestined to have certain definite characteristics entirely regardless of what its environment might be like. The only possibility of any effect by the environment seemed to be in selecting whatever heredity might present to it. Just now we seem to be entering upon a new era; for it has been found that while these genes may be definitely allocated upon the chromosomes, the fact is that environment may affect the behavior of these chromosomes and thereby affect the destiny of the genes. Therefore, environmental factors may affect the hereditary characteristics of organisms through the mechanism which determines the position which genes are to have on chromosomes and thereby, in their positions, the new cells. The mechanism of heredity, which first looked as if it would rule the effect of environment out, now becomes the agent through which environment is seen to act.

Weinstein very aptly stated that it is no more correct to say that the characteristics of an organism are determined entirely by heredity than it is to state that the area of a rectangle is controlled entirely by its altitude. The environment is the second dimension in determining the characteristics of the organism, just as length is the second dimension of a rectangle, which with altitude determines the area.

As was the case in connection with the effect of light upon the metabolism of organisms, so in this case, we have more evidence accumulated as to the effect of the short rays upon the mechanism of heredity than we have of the effects of the visible spectrum of light.

The work of Muller (1925 to date) has been stimulating in showing how *x-ray* may affect the phenomena of crossing over and the production of mutations in *Drosophila*. The publication of new results is occurring almost daily at the present time, for it is possible now by the use of *x-ray* to produce in a few minutes more mutations than have been known throughout the entire previous history of the work on the genetics of *Drosophila*. It is not possible as yet to make generalizations as to these results further than to state that it has been unquestionably demonstrated that a physical factor of the environment may affect the mechanism of heredity in such a way as to determine the hereditary constitution of the organisms which have been exposed to this factor.

Reference will again be made to the effect of physical factors of the environment upon heredity in connection with the chapter on temperature.

The Effects of Light on the Behavior of Animals.—The behavior of animals has become a highly technical branch of physiology and psychology, and will be referred to here only as it relates to the field of ecology, no attempt being made to give a critical consideration of animal behavior. Mast (1911) gives a summary of the general work of the effect of light on the behavior of organisms. Other citations in the bibliography will aid the student in determining the various types of work which have been done in this field.

In considering the behavior of animals with respect to light, it is necessary to distinguish between those organisms which see in the sense of perceiving images, and those which are able to perceive only the difference between light and darkness. Practically all adult insects have eyes which form images, and are therefore able to see. Many of them in immature stages, however, perceive only the difference between light and darkness. In the early history of the development of the theories with regard to the reaction of organisms to light, it was assumed that the organism acted as a machine, being either positive or negative, and that no other reaction was possible. However, our more recent interpretations seem to indicate that these reactions are extremely complicated and cannot be conceived of as simple machines which go toward or away from light, depending only upon the intensity of the light. It seems evident that there are many factors of the environment which control the condition of the organism at the time of the reaction and that may modify the action of light as such.

Light may affect animals by producing a response which may be in the nature of an increase or a decrease or may be, in fact, any change in the activity of the organism. The familiar Bunsen-Roscoe law states that the time of exposure is inversely proportional to the light. This is familiarly expressed in the formula which states, that intensity times time equals a constant ($IT = \text{constant}$). In this case, light is considered as visual intensity. Light of the different wave lengths, however, may have different values in stimulating organisms. It is interesting to compare the results of Laurens and Hooker (1920) in studying *Volvox*, with the results obtained by Mast (1917) in studying the reaction of blow-fly larvae to light (Fig. 10). Laurens and Hooker used the intensity of different wave lengths which were necessary to get a response. The minimum intensity of any light became a measure of its effect upon the *Volvox*. The lower the intensity required for a minimum effect, the greater the effect of that wave length. Mast developed an interesting technique of comparing two converging rays with each other and using the relative intensities of one as compared with the relative intensities of the other in measuring the effect. It is significant to note that with

both of these methods of investigation and with *Volvox* in one case and larvae of the blow fly in another, almost the same point of the spectrum gives the maximum effect (Fig. 10). This is at about 5,000 Angström units. It is to be noted that this is not at the point of maximum intensity to the human eye, but at a point with considerably shorter wave lengths. This is in accordance with the results of Lutz (1924), which seem to indicate that insects are sensitive to shorter wave lengths than is man, therefore seeing more of the violet and possibly farther into the ultra-violet than we can.

Light is an important factor as a medium through which organisms react in seeking food and avoiding enemies. The reactions of insects to light have been studied considerably, and the earlier literature tended to produce dogmatic conclusions with regard to their reactions. Dolley (1916) made a rather careful study of the reactions of *Vanessa* to light, and concluded that many of the former conclusions were not justified. He found that if one of the eyes of the butterfly was blackened, it could still orient itself with the other eye. This does not support the theory that if one eye is illuminated and the other is not, an automatic mechanistic reaction takes place over which the insect has no control. He further showed that with experience they bettered their reactions.

It is also well recognized at the present time that other environmental factors may modify the reaction to light. Minnich (1919) found that while the honey bee is strongly positive in its response to light at ordinary temperatures, this reaction may be reversed at low temperatures.

There is ample evidence to demonstrate that certain insects, at least, react to sight as well as simply to the presence or absence of light. It is possible that some of the literature of natural history has overemphasized the value of sight as such. It is natural to attempt to interpret insects' reactions in terms of human vision, and probably the naturalist of the past erred in this direction. It is also perfectly evident that physiologists have tended to interpret reactions entirely in terms of phototropisms and have neglected all other possibilities in so doing. It is necessary to base judgment on fact, and at the same time not let a few facts influence judgment.

Abbott (1919) in investigating the reactions of certain isopods to directive rays of light concluded that they were usually negative and

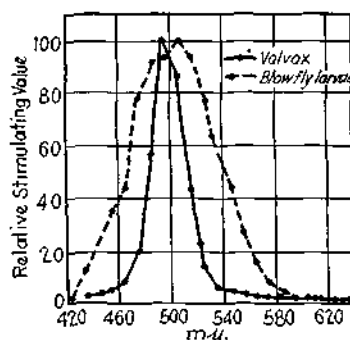


FIG. 10.—The relative stimulating value of spectral lights of equal energy content as ascertained from the determination of the minimal duration of exposure necessary to produce a reaction. (Adapted from Mast, 1917, and Hooker, 1920.)

that this reaction resulted in keeping them in their normal environment, which is under logs and stones. Their prompt reaction to an increase of light was also interpreted as protective, as in a case when logs or stones were removed exposing them to light suddenly.

Allee and Stein (1918) concluded that the reactions of certain aquatic insects were determined by the rate of metabolism of the individual insect. In such a case any environmental factor which might influence the rate of metabolism would also influence the reaction to light. Perhaps we are eventually to come to look upon reactions to light in some such way as this. We may thus see how difficult it would be to draw any valid conclusions from a few observations under set laboratory conditions.

When attention is turned to many of the ecological problems which involve the factor of light upon the seasonal and diurnal activities of insects having a geographic distribution which may be correlated with length of day, with their escape from enemies, and their discernment of food, the difficulty of getting any true evaluations of the situation seems almost staggering. However, the situation is to be interpreted rather as encouraging than discouraging. Even the very field of physics, which is involved in formulating a conception of the constitution of light, is itself still in an uncertain condition. An attempt to write an account of light and its importance in ecology at the present time may be compared to the writing of a single chapter in a continued story, and leaving off when only that first chapter is finished. New publications from results in this field are coming out daily, and some of the results are so startling that when we have finished reading one, we wait almost in suspense for the next.

An attempt has been made to cite the papers of importance which have bibliographies connected with them. It is not contended, however, that these are the most important papers or that all of the important papers are there. However, it will serve as a guide to the student who wishes to go further into the subject of light as an ecological factor.

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CHAPTER III

TEMPERATURE AS AN ECOLOGICAL FACTOR

Attention will now be turned to that portion of radiant energy which lies just beyond the longest wave lengths of the visible spectrum, which we have considered under light; and this is temperature. There is probably no other physical factor in the ecology of animals which has received more attention than has temperature. This is partly because its effects are so very evident, and partly because of the great variation of temperature in time, in both the diurnal and the annual cycles, and in space over the surface of the earth. It probably affects animals more evidently and in more ways than any other factor. The factor itself is measured more easily than any other, and in general the correlation between the changes in temperature and the effect upon the animals is usually very apparent.

It might have been more logical to have headed this chapter "Heat" rather than "Temperature," inasmuch as it follows immediately the consideration of light which is another form of radiant energy. In dealing with heat we would be confined in our measurements to gram calories per square centimeter, as an expression of the quantity of radiant energy. In dealing with temperature we may use the degrees of a thermometer scale. Temperature may be defined as the condition of the body which determines the transfer of heat to or from other bodies. The thermodynamic measurements which we shall deal with in this chapter are on the temperature scale, rather than measurements of the quantity of radiant energy. Consequently, it has seemed wise to deal with it under the heading, Temperature. Indeed, it is this ever-present transfer of energy which becomes one of the most important physical factors of the environment.

General References to Literature on Temperature.—From the point of view of general physiology, we find the effect of temperature well summarized by Bayliss in the last edition of his book. Scattered citations on the effect of temperature upon insects were well summarized by Bachmetjew in 1901 and 1907. It is regrettable that we have no summary of the scattered literature since this monumental work. Such a summary would bring our knowledge down to date. Davenport (1908) summarized literature on animals in general, and tabulated certain critical temperatures for various species. Kanitz (1915) gives a general discussion of the effects of temperature on biological processes mainly

from a purely physiological standpoint. Shelford (1929) reviews methods of measuring and controlling temperature.

Experimental Methods of Measuring Temperature.—Temperature is measured by the change in a physical condition which has been shown to bear a linear relationship to changes of temperature. The thermodynamic scale is independent of the properties of any material substance. It is based solely upon the laws of thermodynamics and is accepted as a standard scale of temperature. On this scale, temperatures are proportional to the pressure or volume of an ideal gas at a constant pressure or volume. When volume is maintained as constant, temperature is proportional to the pressure. When pressure is maintained constant, temperature is proportional to the volume. Absolute zero on the thermodynamic scale is that temperature at which the pressure of a fixed mass of an ideal gas maintained at a constant volume becomes zero.

The usual scales of measurement of temperature are all related to the effect of temperature on water. Fahrenheit obtained a low temperature by the use of ice and salt, and assumed this to be the lowest obtainable temperature and therefore called it 0° . He made an approximation of the temperature of the human body for 100° , though he was not quite correct in this. The freezing point of water was accidentally 32° , and the boiling point 212° . On the Fahrenheit scale, $1^{\circ} = \frac{1}{180}$ of the difference between the freezing and the boiling point of water. On the Réaumur scale, which starts with the freezing point of water as 0° , 1° equals $\frac{1}{80}$ of the difference between the freezing and boiling points of water.

The centigrade scale, which is based on the freezing point of water as 0° and the boiling point of water as 100° , is the simplest and most logical to use for ordinary purposes. However, even this may be misleading for certain phenomena in connection with which a so-called "absolute scale" is used. The absolute zero of the thermodynamic scale is -273°C. , or -459.4°F. It is interesting to note that this "absolute scale" is based upon a theoretical " 0 " arrived at by calculation.

The general consideration of thermometry, together with literature, will be found in "International Critical Tables," volume I, page 52, 1926, and in Wood and Cork (1927).

The expansion and contraction of gases, liquids, and solids and the constants of certain thermo-electric phenomena are the common ones used in thermometry. By far the most common thermometer is the mercury glass thermometer, in terms of which nearly everyone visualizes temperature change. The application of the mercury glass thermometer is limited by the freezing point of mercury at -38.85°C. , and also by its size, which renders it difficult to use in certain inaccessible or very small places. Other liquids, such as pentane, alcohol, and toluene, are often used in the place of mercury. Their properties may be determined

in "International Critical Tables." It is sometimes convenient to make metal thermometers, in which case two strips of metal are fastened side by side, one of them having a higher expansion coefficient than the other. When the temperature rises, the metal with the high expansion coefficient expands more rapidly than the other, which causes the laminated bar of metal to bend, with the metal of the high-expansion coefficient on the convex side and the one of the low coefficient on the concave side. A lever attached to one end of this laminated bar will indicate changes in temperature when a scale has been properly calibrated. This form of thermometer is taken advantage of in many recording instruments.

Thermo-electric methods of measuring temperature are very convenient where precision is wanted, or where temperature is to be taken in an inaccessible place. These, in general, consist of two types: resistance thermometers and thermocouples. The theory of the resistance thermometer is based upon the fact that the resistance which a metal, usually platinum, offers to the passage of an electric current, is proportional to the temperature. Such thermometers may be made with extreme accuracy. The use of such thermometers, however, has the limitation which goes with such laboratory equipment as is required for the extreme accuracy of measurement of resistance to an electric current. It is difficult to make an accurate resistance thermometer for use in a small space. Consequently, they are restricted to certain types of laboratory work requiring accuracy but not demanding measurement in a small space.

The thermocouple method is the most usual and most convenient thermo-electric method employed in ecological work. Robinson (1927) gives a brief description of this principle. Thermocouples depend upon the fact that when two dissimilar metals are joined, an electromotive force is set up at the point of contact, and that the amount of electromotive force is directly proportional to the temperature at that point of contact. This energy apparently represents the excess of electrons emanating from one of the metals as compared with those from the one with which it is in contact. Tables of the thermo-electric properties of metals have been prepared ("International Critical Tables," Vol. I, p. 57). Copper and constantan, an alloy, are very suitable for temperatures within the range of ecological importance and they both have the advantage of being relatively non-corrosive. When two junctions are made and one is held at 0°C. and the other at a higher temperature, the electromotive force from the warmer junction will pass the weaker current from the colder junction, making the measurable current in the system equal to the difference in temperature between the two junctions. Since the temperature of one junction is known to be 0°C. (this couple being surrounded by ice and water), it is necessary to know only the factor

for converting the electromotive force, as read in millivolts, into degrees centigrade. If an ordinary voltmeter is used, the resistance of the wires leading from the couple to the voltmeter will be an unknown factor in reducing the current which reaches the voltmeter or galvanometer.

A number of types of potentiometers and pyrovolters have been designed and manufactured which eliminate the factor of resistance in the circuit and thus make direct readings possible. Thermocouples make it possible to read temperatures in inaccessible places, such as in insect bodies, under the bark of trees, and at various depths in the soil. A series of junctions may be connected with the constantan wire from a cold junction in such a way that any one of the copper wires may be put in connection with the pyrovoltmeter or potentiometer by means of a switch, as shown in Fig. 11. In this way a series of temperatures may be read in succession by simply closing one switch at a time to connect the junction at the point where the temperature is desired to be read.

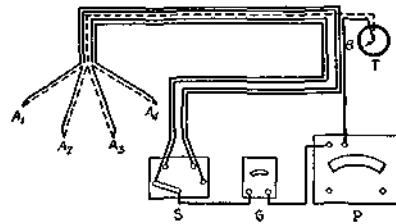


FIG. 11.—Arrangement for multiple thermocouple assembly with warm junctions scattered. (Robinson, 1927.) $A_1 - A_4$ = warm junctions. T = thermos bottle. B = cold junction. S = switch. G = galvanometer. P = potentiometer.

Methods of Recording Temperature.—Various types of thermographs are constructed for meeting almost any requirement of laboratory or field conditions. In general, they are metal- or liquid-expansion thermometers connected with levers and pens for writing the thermographs on a record. The form of the record may be either a disc of paper which revolves, or a strip of paper which is wound about a revolving drum. Some of these instruments are so constructed that the sensitive element may be several meters from the recording instrument itself. The thermo-electric method is coming more and more into use in connection with recording instruments. Commercial firms are now making recording potentiometers and wheatstone bridges which make it possible to have continuous records made at long distances from the sensitive point. The specifications of these machines may be obtained from the catalogs of standard-instrument makers (Shelford, 1929). The apparatus is fairly expensive; but when it is considered that it may record as many as 16 or 18 points, it will be found less expensive than as many separate thermographs.

The computation of the mean temperature from the record is important. Hartzell (1919) has shown that the so-called "mean temperature" computed by averaging the maximum and minimum temperatures for the day is much more apt to give a discrepancy which is positive than one which is negative. The true daily mean temperature is equal to the

altitude of a rectangle, the area of which is equal to the area of the thermograph record from the base 0° . If the record extended below 0° , the negative area would, of course, have to be included in computing the area of the thermograph record. Hartzell concluded that a good approximation for the daily mean temperature may be arrived at by dividing the sum of the hourly temperature by 24. This gives the mean hourly temperature as an approximation of the daily mean temperature. The United States Weather Bureau commonly computes the mean temperature for the day by dividing the sum of the maximum and minimum temperatures by two. This is far from accurate, as the maximum and minimum temperatures are usually attained for only a short period of time. Consequently, the resulting mean as given by the Weather Bureau may be misleading.

Methods of Controlling Temperature.—It is probably true that there has been more equipment installed in biological laboratories for the control of temperature than for the control of any other factor. Various devices have been employed for the production of heat and cold, for the recording of temperature, and for the turning on and off, of the sources of heat or refrigeration. The source of energy for either heat or refrigeration is commonly electricity. Consequently, the thermostat must consist essentially of a switch to turn on and off an electric current, regardless of the sensitive mechanism that may be used in responding to the temperature changes. It is usually not practical to have the thermostat act directly upon the current used for the heat or refrigeration, for the reason that the high voltage will produce an arc when the thermostat is barely in a position of opening or closing. There are several methods of obviating this difficulty. There are several cheap thermostats on the market with rugged points which are able to stand whatever arcking occurs when the current is made and broken.

Another method is the use of a rocking mercury valve. This consists of a glass tube sealed at both ends and pivoted in the middle. One of the contact points is at the center of the tube, and the other at one end. Enough mercury is introduced into the tube to extend from the lower end to the middle when the tube is tilted. The sensitive element of the thermostat is so arranged that it will throw the tube from the position of a tilt in one direction to a tilt in the other direction. This takes place suddenly, and the mercury is poured from one end of the tube to the other. When it is at one end of the tube, the mercury makes the contact between the two electrical points, and the circuit is closed. When the mercury is toward the other end of the tube, the two points are left separate, and the circuit is open.

A third and more usual method of avoiding the arcking of the heavy current is by having a secondary current created by batteries or furnished through a transformer. This secondary current is made and broken

by the sensitive element of the thermostat, and this weak current acts upon an electromagnet which makes and breaks the current on the heating

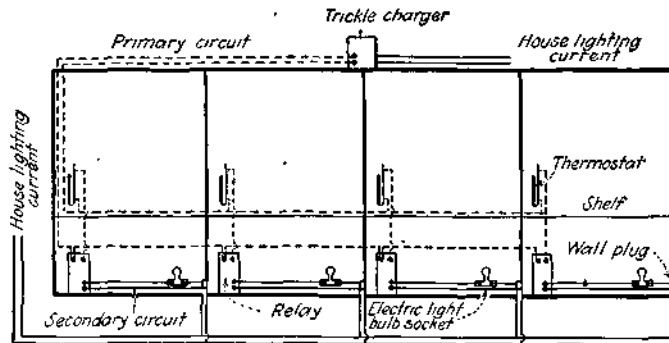
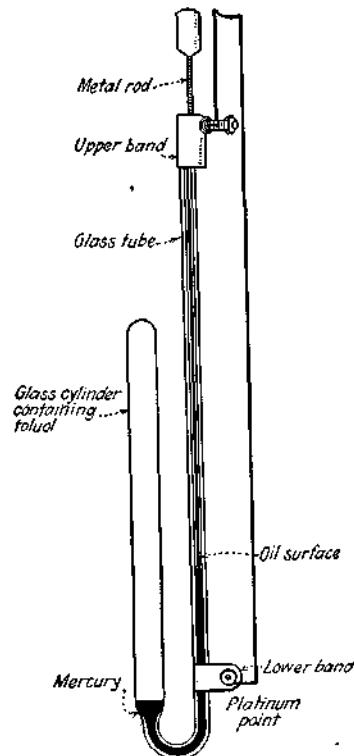


FIG. 12.—Diagram showing electric connections for one or several temperature cabinets (toluol-mercury thermostat). (Robinson, 1928.)

circuit. Robinson (1928) has shown a connection for such a circuit. He also describes a mercury-toluene thermostat which is very successful. This can be made to operate within a small fraction of 1°C ., and is very cheap. Figures 12 and 13 show the circuit for a series of cabinets and also the connection for one of the mercury-toluene thermostats.

Harvey's modification of the Beckman thermometer principle is a very delicate thermostat which has wires projecting into the space occupied by the mercury column. By adjusting the amount of mercury in the bulb, the point at which the secondary current is to be made or broken can be controlled to an accuracy of several hundredths of one degree.

In addition to a sensitive thermostat, it is necessary to have a proper source of heat and refrigeration. Any ideal temperature control must be so arranged that the temperature can be raised or lowered whenever necessary. Heat can be supplied conveniently by either a series of resistance coils or ordinary electric lamps. These may be baffled to prevent the light from interfering with the experiment, if necessary. To get a very careful temperature control, it is necessary



Side View of Thermostat
FIG. 13.—Side view of thermostat. (Robinson, 1928.)

to have a small heating element controlled by the thermostat, and the rest of the heat supplied by manual control. If the thermostat operates a large heating unit, there is apt to be a fluctuation in the temperature curve as the elements go on and off. The air in the cabinet should be circulated to prevent any pocketing or stratification.

There are various methods of producing refrigeration which are described by Kanolt (1924). Where only a slight cooling is required, ice may be used, but with a continual source of inconvenience. Where only very small chambers are to be cooled, it is possible to produce a temperature as low as -54.9° by using proper mixtures of calcium chloride and snow. For freezing point determinations, a Dewar flask may be used. This is surrounded by a vacuum chamber similar to the filler of an ordinary thermos bottle. Material to be frozen may be put in a tube which is projected down into the flask through a cork stopper. The tube may then be surrounded by ether through which air is aspirated. With a little experience, it is possible to produce a very even gradient of temperature reduction. This same apparatus may be used with a copper coil connected to a tube of compressed carbon dioxide with a reduction valve leading to the copper coil. This method is very satisfactory in a room where the relative humidity is low. If the humidity is high, there will be the difficulty of the formation of dew and freezing with the copper tubes.

The most common and convenient method of producing refrigeration for experimental work is by means of the compression and expansion of various liquids in which the heat of expansion and evaporation are taken advantage of. Ammonia, carbon dioxide, sulphur dioxide, and other compounds may be used. The degree of cooling will depend upon the difference in pressure between the high and the low sides of the expansion valve. It must be remembered, however, that the capacity for heat will be governed by the quantity of gas which is circulating through the refrigeration coils. Consequently, if the valve is only slightly open, there may be a great difference of pressure on the two sides of the valve, but the quantity of gas in circulation may be so small that its capacity for removing heat will be greatly curtailed. There are many commercial machines on the market which operate very efficiently and dependably as refrigeration units.

Many devices are described in literature for controlling temperature for ecological research. One of the simplest devices is a long chamber which may be from two or three feet to 10 to 15 feet long, constructed of some good heat conductor. Some of those which are on the market in Europe are made of copper. In one end there is an ice chamber, and at the other end there is a heating unit. These are usually so arranged that small containers may be placed in the chamber various distances between the refrigeration unit and the heating unit. The distance

between the heating and refrigeration units, at which the small container is placed, controls the temperature to which it is exposed.

Figure 14 shows one of the units which is used in the temperature research laboratory of the Division of Entomology at the University of Minnesota. There are a series of six cabinets surrounded by insulation with double glass doors on the top and at the side. Each cabinet has its own mercury-toluene thermostat with the corresponding relays mounted at the end. Each unit operates at a temperature $5^{\circ}\text{C}.$ above or below the adjacent units. All cabinets operating below $27^{\circ}\text{C}.$ are supplied with a coil, through which brine is circulated by a pump con-



FIG. 14.—Temperature cabinets at the University of Minnesota.

trolled by another thermostat system. The temperatures are recorded by a Leads-Northrop multiple recorder, which is shown at the extreme right of the figure. Each cabinet below $27^{\circ}\text{C}.$ has a double system of temperature control, one for refrigeration and the other for heat. Day-light lamps are mounted above the cabinet for use when necessary. Each unit of the system has its own set of manual valves on the brine circulation, and it is possible to set the valves in such a way that the cabinets receive about the right amount of circulation of brine, the pump which circulates the brine being controlled by a thermostat. Refrigeration is, therefore, automatic after the valves have once been set by hand for the desired intervals for each cabinet.

TEMPERATURE AS A FACTOR IN ANIMAL ECOLOGY

Animals are profoundly affected by temperature in many ways. Probably no other single factor has a greater effect upon their geographic distribution on the earth, or upon the periods of their activities during the annual cycle. Within the limits of temperature in which they are active, the rate of their metabolism and consequently their rate of growth and reproduction and the resultant population are controlled. Their behavior, their form and structure, and even the mechanism of heredity, all come within the influence of this general and far-reaching environmental factor. The influence of temperature extends even farther than this, in that it affects nearly all of the other physical factors of the environment. The moisture in the air, the pressure of gases, and the movement of the air must all be interpreted in terms of the temperature which is operating at the time. In evaluating physical factors it is probably a correct generalization to state that light affects temperature, and temperature affects everything else.

General Effects of Temperature upon Animals.—Animals with regard to their relationship to temperature fall into two natural groups. One, the poikilothermic or cold-blooded animals, has no precise mechanism for regulating the temperature of their bodies. Consequently, their body temperatures follow more or less closely that of the surrounding medium. The other group, the homiothermic or warm-blooded animals, has a mechanism which maintains the temperature of their bodies more or less constant and independent of the surrounding medium. The group of homiothermic animals includes the mammals and the birds which are set apart from all other animals in that they essentially carry their environmental temperature with them.

The ability to regulate temperature is developed very early in the ontogeny; and as Kendeigh and Baldwin (1928) have shown, nestling wrens at first are poikilothermic, but very soon become homiothermic. Certain of the mammals which hibernate to conserve energy during the cold weather become essentially poikilothermic during that period, as will be described under the heading of Dormancy.

Insects are all poikilothermic. There are, however, certain interesting exceptions in connection with some of the social insects. The honey bees are able to maintain their temperature as a colony, though individually they are not. A colony of bees, then, looked upon as an ecological unit, might be considered homiothermic. They rear their brood at a more or less constant temperature and also control the temperature of the colony within certain limits during the winter. Many social insects control the temperature of their immediate environment by conserving the heat from their metabolism. Hase (1926) found that the larvae of the wax moth were able to maintain the temperature of their immediate surroundings at 11 to 17° above that of the laboratory.

It is not strictly true that the body temperature of poikilothermic animals varies with the temperature and is always the same as the temperature of the surrounding medium. During the time of activity a certain amount of energy is continually being transformed into heat in the body; and as long as the rate of radiation from the body is less than the rate of production of heat within the body, it follows that the body temperature will necessarily be somewhat above that of the surrounding medium.

Rogers and Lewis (1916) found that the temperature of most poikilothermic vertebrates was very close to the temperature of the surrounding medium, with a slight lag in the larger forms. Pirsch (1923) measured the temperature of the honey bee and found that they tended to be slightly warmer than air at low temperature as long as they were active. At high temperatures they maintained themselves slightly below the temperature of the environment, presumably by increased evaporation. Their ability to maintain their body temperature below that of the surrounding air, however, was very much limited. When they could no longer resist the high temperature, death followed, and the temperature of the bees then assumed the temperature of the surrounding air. Poikilothermic animals are active only within certain limits of temperature above and below which they are inactive. Various terms have been proposed to designate these limits of activity. Possibly the most accepted and expressive terms are the minimum effective temperatures for the lower point of activity, and the maximum effective temperatures for the upper limits of activity.

Shelford (1927) uses the term, "temperature threshold"; and other authors have proposed the term, "developmental zero." The latter term is not very acceptable because it implies that there is no metabolism going on, which is obviously incorrect. Below the minimum effective temperature, life continues in a temperature zone of dormancy. At a still lower temperature, dormancy is terminated by death, at a point which may be called the absolute minimum temperature. In a similar way, life continues above the maximum effective temperature in the state of dormancy, where there are no outer manifestations of activity. Again, a greater extreme of temperature produces death at the point representing the absolute maximum temperature.

A further consideration of the conditions of dormancy due to extremes of temperature will be taken up under the heading of Dormancy.

Between the limits of minimum and maximum effective temperatures, there is a zone in which poikilothermic organisms are active. Somewhere within this zone, there is a point which may be termed the optimum temperature, where life is at an optimum, not necessarily with respect to rates of processes but at which conditions are generally most favorable for the organism. It is difficult to formulate a precise definition of

optimum temperature. Probably the most significant definition would be this: that the temperature at which there is the least environmental resistance to the biotic potential of the organism is the optimum temperature (see page 183).

Effects of Temperature on Physical and Chemical Processes.—Before entering upon a discussion of the effect of temperature on biological processes, it will be well to pause and consider briefly the nature of the effects of temperature on the physical and chemical processes of the structure of an organism.

It is hardly necessary to state that temperature has a profound effect upon all physical processes for, as a matter of fact, our knowledge of temperature is based upon the changes of physical processes, as for example, the volume of mercury under different temperature conditions. One has only to scan the pages of the "International Critical Tables" to see how widespread this effect is. There have been many attempts to formulate a precise equation to express the nature of the effect of temperature upon these processes.

Van't Hoff (1884) made a statement of the general principle of the effect of temperature on chemical reactions, which has since then often been cited in literature as "Van't Hoff's law," although it was nothing new at the time that he stated the principle, nor did he intend at the time to state anything which would be formulated as a law. This seems to be a good example of how the statement of an eminent man may be made into a dogma by subsequent students. In his lectures in Berlin, Van't Hoff referred to this relationship of temperature to chemical reaction with the simple statement that by far the larger portion of reactions seemed to fall between a doubling and trebling as the result of a rise of 10°C. It is true that he gave it formal expression as:

$$\frac{K_t + 10}{K_t} = 2.$$

He then expressed this logarithmically in such a way as to take care of any other difference than 10°C., and reduced it all to a 10° basis. He gave the example of the saponification of ethyl acetate by soda, which solved for a value of 1.89, and followed this by the statement that, while the great majority of reactions took place with a quotient of 2 or 3, the table which followed would show the general range. In this table he gave examples which varied all the way from 1.2 to 7.14. It seems perfectly evident, therefore, that he had no intention of interpreting this as a law, but simply as a general principle which varied within wide limits.

However, the amount of increase of a chemical reaction for 10° is now designated as Q_{10} , and supposed to have a value of 2. This Q_{10} is almost a sacred number in the literature of physiology.

Arrhenius (1889) proposed a formal expression of this same relationship based upon the absolute temperature scale by introducing a constant, the function of which is to bring Q_{10} more closely to a value of 2. He wrote the expression $K_1 = K_0 e^{\frac{\mu}{2} \left(\frac{T_1 - T_0}{T_1 T_0} \right)}$. In this expression T_0 and T_1 are the two temperatures reckoned from the absolute temperature scale. K_0 is the velocity of the reaction at the lower temperature T_0 , and K_1 is the velocity at the higher temperature T_1 . The Greek letter μ is the constant, which is introduced to make the ratio 2, which is the numerator of this fraction, a constant. The value of μ for most biological processes ordinarily lies between 12,000 and 16,000. He also said that there was no essential difference existing between the processes studied in general chemistry and those produced by living organisms or enzymes as measured by the values for μ .

This method of comparing the rates of biological reactions with those of chemical reactions has been seized upon by various physiologists, and the value of μ , or the letter q , as it is sometimes written, has been used for examining the nature of various physiological reactions. Snyder (1911) in commenting upon this type of work states:

Remembering at the same time that Prof. William Ostwald has referred to the influence of temperature upon chemical reactions as "one of the darkest chapters in chemical mechanics," what shall we say of temperature and its influence upon physiological action . . . The present author believes that the matter is more complex than that of chemical reaction, as dark as that may be.

Proponents of the theory contend that chemical reactions may be compound reactions, and that during a portion of the reaction one of the component parts may constitute a master reaction. During another portion another component reaction may be the master, the result being that the curve of the velocities would not be a simple curve, but a compound curve. Different portions of it would have to be considered differently, and consequently there is no reason why the simple Q_{10} should apply throughout the entire length. Therefore, the value in Arrhenius' equation for μ would have to be changed depending upon the master reaction controlling the compound reaction at any particular time. It seems, therefore, that many physical or chemical reactions are so complex that it is difficult to make a simple formula approximating the nature of the effect of temperature applied to them very generally. Q_{10} values, as ordinarily quoted in literature, have no statistical value at all. This can best be appreciated by referring to Van't Hoff's table, where the values run from 1.2 to 7.14. This must be borne in mind in turning attention to the effects of temperature upon biological processes.

Effects of Temperature on Biological Processes.—Turning attention now to biological processes, which, as has already been stated, rest upon

a physical structure which should obey the physical laws; we have a case which is even more complicated than that which has just been considered under physical and chemical processes.

In comparing the activities of an organism with the rate of physical and chemical processes, we might make a distinction between the basal metabolism of an organism, which may be compared quite directly with a physical and chemical process, and the general activity of an organism including the search for food, reproduction, and so on. In measuring the oxygen consumption or carbon-dioxide output of a quiet organism, we have a process which is quite comparable to that of the more complicated physical and chemical reactions. But when we have an organism which spends part of its energy in the search of food and in reproduction, we have added to our simple process the activity which insures that the process will go on. Energy, therefore, is being used for the getting of food to make sure that there will be material for oxidation and for reproduction, insuring that there will be a mechanism for carrying on the oxidation in another generation. The basal metabolism of the quiet organism is very likely a matter of purely physiological consideration, though of importance to ecology. The total activity of the organism is of importance to ecology directly, and is a matter primarily for ecological consideration.

The fact that there is a general quantitative relationship between the activities of organisms and the temperature has been recognized for centuries. Réaumur (1736) recognized that there was a quantitative relationship and suggested that the total heat as expressed in temperature summations required to produce complete growth was a constant. In making these summations, Réaumur used all of the temperature above zero on his thermometer, which means all temperatures above the freezing point of water. Von Oettingen (1879) recognized the straight-line relationship and introduced a definite point on a temperature scale to represent zero not as the freezing point of water, but as a threshold of development for the organism. Since this time there have been a series of investigators attempting to formulate a principle which would state definitely the linear relationship of the rates of biological processes to the temperature scale. These have been recently well summarized by Peairs (1927) and Ludwig (1928).

In 1913 Sanderson and Peairs published rather extensive data on the effect of constant temperature on rates of insect development, showing that the reciprocal of the time-and-temperature curve was a straight line and that above the threshold of development time multiplied by time temperature gave a constant. The next year Krogh (1914) published his generalizations based on the rates of processes in various types of animals and formulated a principle which has since often been spoken of as Krogh's law. He concluded that Vant Hoff's and Arrhen-

ius' principles did not give a good approximation to the rates of biological processes, and he advanced the formula:

where $V_t + 10^\circ = V_t + K10$,

V represents the velocity at any one temperature, and

K is the increase in velocity,

$K10$ being the increase in velocity 10°C .

This statement differs from that of Van't Hoff in that the constant is added, instead of being multiplied, to the rate at one temperature in order to obtain the rate at a higher temperature. This means that an increase of 1°C ., within certain limits, always produces the same acceleration in rate of development. The limits within which this straight-line relationship applies are usually spoken of as the limits of normal development. The time temperature curve is, within these limits, a hyperbola, and the rate temperature curve is a straight line. It was not contended by Krogh, and possibly by no one else, that this rate temperature line was straight throughout the entire temperature scale, or even down to the minimum effective temperature or threshold of development. Krogh showed that as the threshold of development was approached the line of actual development deviated above the theoretical line, and that at higher temperatures it deviated by dropping below the theoretical straight line.

Jacobs (1928) reviewed the possibilities of applying a definite rule to processes which are involved in the physiology of organisms, and showed how impossible it is to expect such expressions as those of Van't Hoff and Arrhenius to apply to many processes which are involved in the physiology of animals.

Peairs (1927) and Ludwig (1928) have shown that of all the generalizations with regard to the relationship between velocity of biological processes and temperature, the principle as expressed by Sanderson and Peairs (1913) and Krogh (1914) is probably as good a generalization as any. Ludwig showed that the adaptation of Arrhenius' formula by Crozier (1924) cannot well be applied at least to the Japanese beetle (*Popillia japonica* N.). The following table from Ludwig shows the values for μ obtained for the various stages in the life history of this beetle. These values according to the formula of Arrhenius as used by Crozier should be constant, but it will be noticed that they vary from a $-27,000$ to a $+66,000$ and that in one stage, that of the second instar, they vary from a $-6,175$ to a $+65,298$. These variations in the value of μ are often interpreted as indicating that different master reactions are obtained during the different stages of the life cycle.

Bayliss (1924) points out that there are many processes, such as diffusion and adsorption which take place simultaneously with the chemical processes, and states that the velocity of the process as a whole

TABLE I.—VALUES OF μ OBTAINED FOR THE JAPANESE BEETLE¹

Temperature, °C.	Egg	First instar	Second instar	Third instar	Pupa
13 -15	44,914
15 -17.5	43,225	32,707	33,215
17.5-20	29,734	66,565	26,065
15 -20	65,298	-
20 -22.5	24,117	35,046	24,462	-27,105	19,934
22.5-25	20,352	11,255	33,912	-18,002	19,207
25 -27.5	11,088	9,175	- 439	14,523
27.5-30	12,211	124	-6,175	7,321
27.5-31	8,676
30 -32.5	6,175
30 -33	-259
32.5-35	-8,909

¹LUDWIG, *Physiol. Zoology*, vol. I, no. 3, p. 379, 1928.

may be conditioned by the factor which takes place at the slowest rate. In many cases this might be diffusion. It is known, of course, that during the pupal stage, for instance, the processes going on are quite different during histolysis and histogenesis. It is difficult, however, to understand why a second instar larva might have a μ value at temperatures from 15 to 20° of 65,000 and a μ value of -6,000 at 27°.

Janisch (1925) and others have attempted to construct exponential curves which would aid in interpreting the data in terms of straight-line relationships with deviations above and below the so-called "normal limit."

All of these attempts to get an empirical relationship expressed mathematically may be looked upon as of purely physiological interest and merely as attempts to approximate the effects of temperature on very complicated processes. Attention will now be called to the use of the principle of Krogh (1914) or of Sanderson and Peairs (1913) in ecological work, the assumption being that the principle was at least usable.

The following graph of Krogh's (1914b) experiment with developing frog's eggs will serve to illustrate a number of facts with regard to this principle. This curve is based upon the time required for certain changes in segmentation to take place. It will be noted that all of the points between 7° and 20° lie on the straight line. If the straight line is extended downward, it will intersect the axis of the abscissa at 2.7°C., which will mean that, theoretically, no segmentation could take place at this temperature. By using this point and letting x = temperature in degrees centigrade and letting y = the time factor, we may express the value of the points on the time temperature curve as $(x - 2.7)y = K$.

Krogh's curve shows that the rate of segmentation deviated from the straight line at about 7° and that the rates at lower temperatures

were greater than might be anticipated. This is generally true of biological processes and means that the value 2.7° for the minimum effective temperature, which may be arrived at by projecting the straight line, is not a true value for the point at which the process will stop. Shelford calls this theoretical point the "a" point. It is important to note, however, that this theoretical point can be used in calculating a constant for points on the hyperbolic curve, while the true minimum effective temperature (threshold temperature) could not be used in this way because it lies outside the hyperbolic curve.

At the upper end of the curve there is likewise a deviation from the straight line. This is to be expected if we recognize an optimum temperature and a maximum effective temperature as separated on the temperature scale. The point at which the curve deviates from the straight line will approximate the optimum temperature, beyond which the process is slower than would be anticipated on the basis of the rates of development at the lower temperatures. The temperature at which the development stops would obviously represent the maximum effective temperature. Krogh's curve further illustrates the inadequacy of Van't Hoff's principle in even approximating the rates of development. The values of Q_{10} for the process of segmentation in the frog's eggs are compared with the values for the constant as computed from the time and effective temperature in the following table:

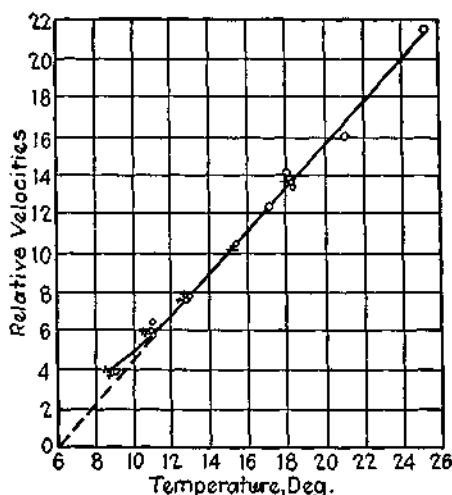


FIG. 15.—Graph of the temperature-velocity relationship for the development of frog eggs (Krogh, 1914.)

Q_{10} Values of Van't Hoff

$$3-5^{\circ}Q_{10} = 5.3$$

$$5-10^{\circ}Q_{10} = 4.1$$

$$10-15^{\circ}Q_{10} = 3.0$$

$$15-20^{\circ}Q_{10} = 2.0$$

K Values of Krogh

$$7.7^{\circ}(x - 2.7)y = 2,410$$

$$10.2^{\circ}(x - 2.7)y = 2,490$$

$$12.55^{\circ}(x - 2.7)y = 2,303$$

$$16.9^{\circ}(x - 2.7)y = 2,325$$

It will be noticed that the Q_{10} values decrease from 5.3 at the lower temperature to 2 at the higher temperature, while K constant of Krogh remains relatively constant throughout the entire range. Illustrations of the application of this principle may be found in Sanderson and Peairs (1913) and Peairs (1927).

Attention must be called to the fact that each stage of the life cycle of an organism may have separate temperature characteristics. This is well illustrated in the study which Ludwig (1928) made of the Japanese beetle. Table II gives the value for the constant times' temperature minus the threshold value for the various stages of the life cycle for the temperature range in which it normally lives. It is important to note that the third instar is dependent for its length not only upon temperature, but upon the length of the other instars. When the other

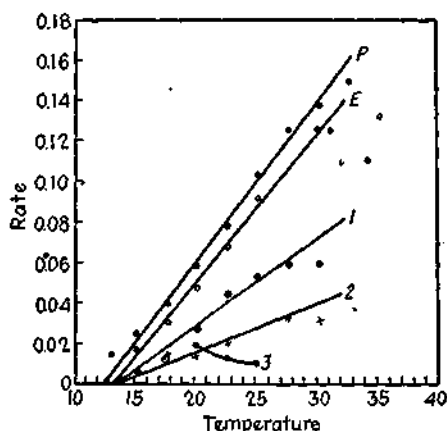


FIG. 16.—Comparison of the rates of development of each stage of the Japanese beetle. (Ludwig, 1928.)

instars are long, it is relatively short, and when they are relatively short, it is relatively long. This is probably due to a nutritional and maturity factor which will be referred to later in the chapter on nutrition. In no two stages are the values for the day-degrees the same. And when the day-degrees for the entire life cycle are totaled, the values are slightly different for each temperature. The following figure, which is taken from the complete data of Ludwig, shows how the values for rates of development at each temperature conform to the straight line. Each stadium

of the life history has a different temperature coefficient, as is shown by the inclination of the straight line.

TABLE II.—DAY-DEGREES REQUIRED FOR THE COMPLETE LIFE-CYCLE OF THE JAPANESE BEETLE¹

Stage	20°C.	22.5°C.	25°C.
Egg.....	146.3	141.5	133.2
First instar.....	245.1	201.0	221.9
Second instar.....	456.9	448.2	351.9
Third instar.....	340.6	676.8	1,141.9
Pupa.....	128.2	129.0	122.0
Total.....	1,317.1	1,596.5	1,970.9

¹ Ludwig, *Physiol. Zool.*, vol. I, no. 3, p. 384.

The difference in the temperature characteristics of the different stages of the same organism is a general one. In fact, it is probably true that the same stage of different insects may be more alike than the different stages of the same species.

Another example is illustrated in the study of grasshoppers. In the following graphs (Figs. 17, 18, 19, 20), the curves of time and temperature, as well as the reciprocals, are shown for the different stages

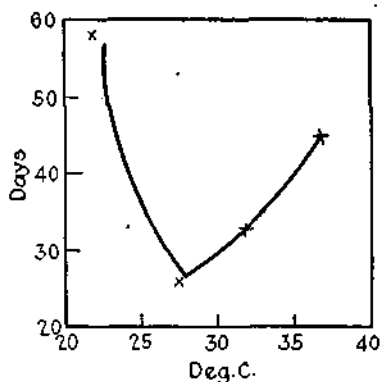


FIG. 17.—Time-temperature curve for the development of eggs of *Melanoplus mexicanus mexicanus* (Grasshopper). (Parker, 1930.)

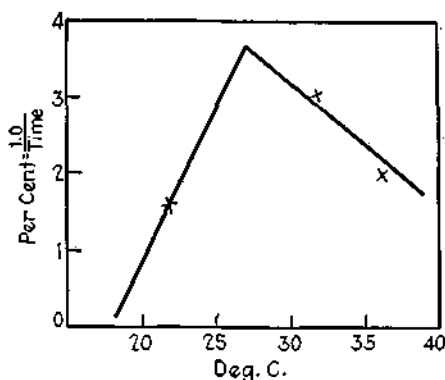


FIG. 18.—Velocity-temperature curve for the development of eggs of *Melanoplus mexicanus mexicanus*. (Parker, 1930.)

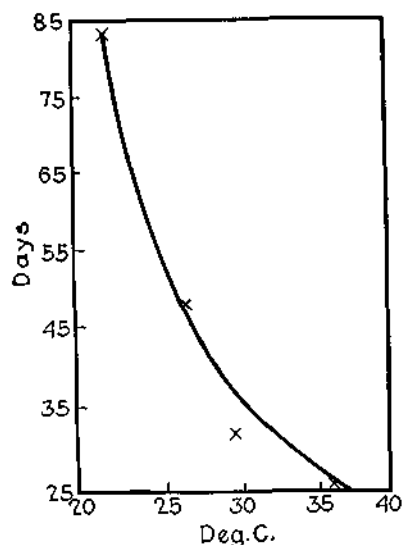


FIG. 19.—Time-temperature curve of development of nymphs of *Melanoplus mexicanus mexicanus*. (Parker, 1930.)

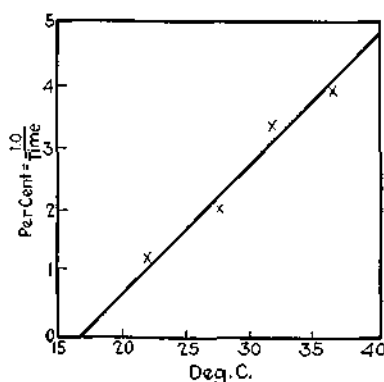


FIG. 20.—Velocity-temperature curve of development of nymphs of *Melanoplus mexicanus mexicanus*. (Parker, 1930.)

in the life cycle of a grasshopper, *Melanoplus mexicanus*. It is evident from these that the rates of development for the different stages of the same species may be so different that it will be necessary to make separate calculations for each stage. The time- and temperature-development

curves for the eggs and nymphs of *Melanoplus mexicanus* are taken from Parker (1930). The data on the hatching of the eggs are interesting, as the optimum temperature is at about 27°, and above this point the time is lengthened and the curve representing this prolongation of time of hatching is a hyperbola. There is only one point below 27°, but this point taken with 27° indicates a minimum effective temperature of 18°C., which substantiates laboratory experience.

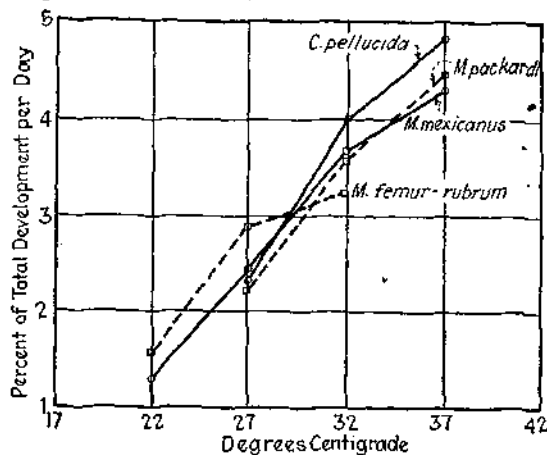


FIG. 21.—Rates of nymphal development of four species of grasshoppers at constant temperatures of 22°, 32° and 37°.

The time of hatching at the various temperatures is the average time in each case. At 22° the time varied from 42 to 100 days (probable error +3.879), at 27° from 23 to 28 days, at 32° from 21 to 38 days, and at 37° from 23 to 68 days. The rate was most uniform at 27° where conditions were optimum, and the greatest variation came at the higher and lower temperatures.

The data on nymphal development do not indicate a definite optimum, although there is a deviation from the reciprocal of the time-temperature curve at the higher temperatures. The values for Q_{10} and the constant $[(x - 17)y]$ are given to show the relative constancy of the two values for the nymphal development of *Melanoplus mexicanus*.

$$22^\circ \text{ constant} = 425$$

$$27^\circ \text{ constant} = 490$$

$$32^\circ \text{ constant} = 450$$

$$37^\circ \text{ constant} = 500$$

$$22-27^\circ Q_{10} = 3.46$$

$$27-32^\circ Q_{10} = 3.26$$

$$32-37^\circ Q_{10} = 2.40$$

In this case the maximum difference in the values for the constant is 75, which is 11.9 per cent of its mean value. The maximum difference in the values of Q_{10} is 1.06, which is 34 per cent of its mean value. Therefore, Krogh's approximation is better than the Q_{10} of Van't Hoff.

Shelford (1927) proposes a developmental unit based upon the differences between the amount of development in one hour at one temperature and the amount of development in one hour at one degree higher temperature. He terms this the developmental unit of one hour of one degree of mean medial temperature, defining medial temperature as that temperature within which the temperature-rate curve is a straight

line. This is a convenient unit for use in making calculations of the effect of out-of-door temperature. It is possible to obtain a mean hourly temperature throughout the period and then apply the unit for one degree of mean medial temperature to the temperatures out of doors. This will be returned to under the consideration of the effects of climate upon insects.

Bodenheimer (1924) calls attention to the formula of Blunck as being a new expression for the relationship of time and development. It is, however, an expression of the same fundamental nature as that involved in Sanderson, and Peairs, and Krogh and the expressions of many others.

The validity of work done with constant temperatures is often called into question from the point of view of ecology, for the reason that temperatures in environments usually are not constant. Probably the time has not yet arrived for making generalizations with regard to the effects of alternating temperatures on animals in general. It is certain that the evidence before us at the present time is not all in agreement. Shelford (1929) states that

the crucial variable-temperature experiments must be done with minimal medial temperatures occurring at night and with temperatures rising to maximal medial during the day. These experiments will usually show an acceleration of development as compared with constant temperatures of the same numerical value as the mean of hourly readings of the variable temperatures.

In the codling-moth pupa the acceleration amounted to 7 per cent, as shown by a decrease in the developmental total.

Ludwig (1928), as a result of his study on the Japanese beetle, drew certain conclusions with regard to the effect of alternating temperatures upon this insect. He says that the effect produced by alternating temperatures depends upon the temperatures involved.

1. If one of the temperatures is above the optimum of development and the other is between the threshold and the optimum, the rate is retarded.

He believes this can be explained by the assumption that in general the rate of development is retarded at temperatures above the optimum. Therefore, when all the rates are taken into consideration, there is a general slowing due to a sort of algebraic sum of a series of rates, all of those which are lying above the optimum showing a retardation.

2. If both the temperatures alternating are between the threshold and the optimum of development, neither an acceleration nor a retardation of rate is produced.

3. If one of the temperatures involved is below the threshold of development and the other is between the threshold and the optimum, the rate is accelerated . . . However, if the threshold temperature is used as a minimum in the calculation of the mean-constant temperature, the rate falls on a straight line.

It is, of course, true that wherever the threshold or minimum effective temperature is involved, the question may be raised as to whether

or not the true threshold value is known and whether there may not have been some development at temperatures below that at which it is assumed that development stopped. Ludwig believes that his generalizations may help to explain some of the apparent contradictions in the results of various investigators, since most of these people work under field conditions where the temperatures involved usually go below the minimum effective or threshold values. There is, however, certain evidence which seems very dependable and which cannot be harmonized with the conclusions of Ludwig.

There seems to be no better example than the data of J. R. Parker.

TABLE III.—COMPARISON OF THE RATE OF DEVELOPMENT OF *M. mexicanus* NYMPHS AT CONSTANT AND ALTERNATING TEMPERATURES

Some nymphs held at constant temperatures from time of hatching until they became adult; others held at a low temperature for 16 hours daily, and at higher temperatures for eight hours daily. Twenty nymphs used for each set of temperatures.

CONSTANT TEMPERATURES										
Temp., °C.	Days in nymphal stage				Percentage of total nymphal development per day					
22	85				1.176					
27	49				2.040					
32	30				3.333					
37	25				4.000					

ALTERNATING TEMPERATURES										
16 hr. daily at low temp. 8 hr. daily at high temp.	Low temp.		High temp.		Total per cent development at const. temp. rate	Theoretical days in nymphal stage at const. temp.	Actual days in nymphal stage at altern. temp.	Per cent development per day at const. temp.	Per cent development per day at altern. temp.	Per cent increase in rate of development at altern. temp.
	Days	Development per cent	Days	Development per cent						
22 and 27	40.00	46.80	20.00	40.80	87.60	68.5	60	1.46	1.66	13.7
22 and 32	32.66	38.21	16.33	54.37	92.50	52.9	49	1.89	2.04	7.9
22 and 37	27.33	31.97	13.66	54.64	86.00	47.3	41	2.11	2.44	15.6
									Average	12.4
12 and 27	71.33	0	35.66	72.74	72.74	147.0	107	0.68	0.93	36.7
12 and 32	40.66	0	20.33	67.69	67.69	90.0	61	1.11	1.64	47.7
12 and 37	32.66	0	16.33	65.32	65.32	75.0	49	1.33	2.04	53.3
									Average	45.8

In this case nymphs of the grasshopper, *Melanoplus mexicanus*, were used in the experiment. All conditions other than temperature were maintained as nearly constant and equal as possible. A condition of alternat-

ing temperature was simulated by keeping the grasshoppers for eight hours at a higher temperature and for 16 hours at a lower temperature during each 24-hour period. The nymphs were hatched from eggs collected in the fields in the same locality, and were divided into lots of 20 each, and exposed to the conditions of the experiment. Four lots were held respectively at constant temperatures of 22, 27, 32, and 37°C. for 24 hours each day. The other lots were so divided that three were kept for 16 hours at 22°; and then one of the lots for eight hours at 27°; another for eight hours at 32°; and another for eight hours at 37°. This was to simulate a night at 22°C. with days at the three temperatures described. Three other lots were held at 12°C. for 16-hour periods; and then given eight-hour periods at 27, 32, and 37°, respectively. Table III gives Parker's results for these experiments. In this table the author has summed up the total time spent at the low temperature and the total time spent at the high temperature, and then has evaluated this time in per cent of development on the basis of the constant-temperature experiments. When the per cents of development for the sum of all the nights and the sum of all the artificial days are added together, he obtains not 100 per cent of development but considerably less.

The per cent of increase in rate of development, as given in the table, is arrived at by taking the difference between the per cent of development per day at constant and at alternating temperatures on a percentage basis. In the case of *Melanoplus mexicanus* nymphs, the threshold temperature is 17°. Consequently, the second series was exposed to temperatures lower than the threshold temperature; and the acceleration was much greater than that of the first series, which was exposed to a temperature of 22° and presumably never ceased development. The case of Parker's data on the hatching of eggs is perhaps an even better example of the effect of alternating temperatures than the one just cited for the nymphs.

The grasshopper eggs used in these experiments were collected from the field in the spring, and then exposed to the experimental conditions described. The general principle involved in these experiments is exactly like that used with the alternating temperatures on grasshopper nymphs. Two species of grasshoppers were involved, and it will be noticed that the general nature of the effect was the same in the case of both species. The per cent of acceleration when 22° was used in a 16-hour artificial night was less than that when 12° was used for the artificial night. The per cent of acceleration, however, is so great that it seems to leave little doubt as to what happened in this series of experiments. (See Table IV taken from Parker, 1930.)

The acceleration found in the experiments with the eggs is very much greater than that found in the experiments with the nymphs of the grasshoppers. This may be explained on the basis of the past history

of the eggs. They were laid during the previous summer, were in the soil over winter exposed to various low temperatures, and then collected in the spring. It was found that if the eggs of *Melanoplus mexicanus* were placed at 0°C. immediately after they were laid, and then later exposed to higher temperatures of 27, 32, and 37°, they developed much

TABLE IV.—COMPARISON OF THE RATE OF DEVELOPMENT OF *M. mexicanus* AND *C. pellucida* EGGS AT CONSTANT AND ALTERNATING TEMPERATURES

Over-wintered field-collected eggs kept at constant high temperatures until hatched. Some also held at low temperatures for 16 hours daily and at higher temperatures for 8 hours daily. Two hundred eggs used for each set of temperatures.

CONSTANT TEMPERATURES										
<i>M. mexicanus</i>						<i>C. pellucida</i>				
Temp., °C.	Days to hatch		Per cent develop- ment per day		Days to hatch		Per cent develop- ment per day			
22	13		7.69		13		7.69			
27	7		14.29		8		12.50			
32	5		20.00		6		16.66			
37	4		25.00		5		20.00			

ALTERNATING TEMPERATURES, <i>M. mexicanus</i>										
16 hr. daily at low temp. 8 hr. daily at high temp.	Low temp.		High temp.		Total per cent dev. at const. rate	Theo- retical days to hatch at const. temp. ¹	Actual days to hatch at altern. temp.	Per cent dev. per day at const. temp.	Per cent dev. per day at altern. temp.	Per cent increase in rate of dev. at altern. temp.
	Days	Per cent dev. at const. temp. rate	Days	Per cent dev. at const. temp. rate						
22 and 27	5.33	40.9	2.67	37.9	78.8	10.1	8	9.9	12.5	26.2
22 and 32	4.00	30.7	2.00	40.0	70.7	8.4	6	11.9	16.6	39.4
22 and 37	3.33	25.6	1.67	41.75	66.3	7.5	5	13.3	20.0	50.3
									Average...	38.6
12 and 27	9.33	0	4.67	66.3	66.3	21.1	14	4.7	7.1	51.0
12 and 32	6.00	0	3.00	60.0	60.0	15.0	9	6.6	11.1	68.1
12 and 37	5.33	0	2.67	66.7	66.7	12.9	8	8.3	12.5	50.6
									Average...	56.5

<i>C. pellucida</i>										
22 and 27	6.00	46.1	3.00	37.5	83.6	10.7	9	9.3	11.1	19.3
22 and 32	4.67	35.9	2.33	38.8	64.7	9.3	7	10.7	14.2	32.7
22 and 37	4.00	30.7	2.00	40.0	70.7	8.4	6	11.9	16.6	39.5
									Average...	30.5
12 and 27	9.33	0	4.67	58.3	58.3	24.0	14	4.1	7.1	73.1
12 and 32	6.77	0	3.33	55.4	55.4	18.0	10	5.5	10.0	81.8
12 and 37	6.00	0	3.00	60.0	60.0	15.0	9	6.6	11.1	68.1
									Average...	74.3

¹ Theoretical days to hatch at constant temperature rate =

$$\frac{\text{actual days to hatch at alternating t.} \times 100}{\text{total per cent of dev. at constant t. rate}}$$

more rapidly than they did when placed directly at these constant temperatures. The acceleration found varies directly with the constant high temperature to which the eggs were returned, and amounted to over 136 per cent at 27°, 357.5 per cent at 32°, and 558 per cent at 37°. The acceleration increased at all three temperatures with the length of time exposed to the low temperature until a period of 242 days was reached. Exposing the eggs to 0° for from 240 to 500 days resulted in only a very slight increase in the rate of development. When the eggs were partially developed before they were exposed to low temperature, there was also an acceleration; but in this case the maximum acceleration was reached at about 60 days instead of 240 days, as in the case when undeveloped eggs were placed at low temperature.

A comparison was made by Parker between the effect of exposing partially developed eggs to 0°C. for a period of time before returning them to a high temperature, and exposing another lot to 8°C. before returning it to a high temperature. It was found that the acceleration was greater when exposed to 0° than when exposed to 8°. It would be difficult to explain these results on the assumption that some development went on below the minimum effective temperature, for those which were exposed to the lowest temperature had the greatest acceleration.

Parker's results on the effect of temperature on the eggs of grasshoppers are of great ecological significance. These grasshoppers lay their eggs during the latter part of the summer and early fall. Some of the eggs go through considerable embryonic development before cold weather arrives, but in the spring they all hatch at approximately the same time. In the experiment it was found that exposure to low temperature for about 60 to 240 days gave the maximum acceleration. Beyond that period of time it made little difference. This is approximately the length of time that these eggs are exposed to low temperature in nature. Since the hatching of eggs is retarded by temperatures above 27°C., those eggs which are laid relatively late in the summer or early in the autumn and are exposed to high temperatures are retarded, and later are accelerated by the low temperature of the winter. Furthermore, the eggs which develop during late summer are accelerated the least by low temperature, and *vice versa*. The result is that nearly all eggs are brought out at about the proper time in the spring.

It is possible to look upon the question of the effect of varying temperatures as the normal effect, and that of constant temperatures as abnormal. From this point of view, it would seem more logical to speak of the retarding effect of constant temperature, rather than of the stimulating effect of alternating temperatures. There are, however, a large group of organisms which live in environments which are very constant in temperature as, for example, organisms living in the bottom of deep lakes. It is very possible, therefore, that it will not be wise

to make generalizations which supposedly apply to all animals until we know more about the effects of temperature on these forms.

Dawson (unpublished thesis) found that alternating temperatures apparently had little effect upon the cocoons of certain moths, which are ordinarily exposed to great variations of temperature. It seems most likely that some ecological grouping will be made of organisms, and it will be found that temperature behavior will vary with ecological conditions. This is a promising field of research for the future. The varying temperatures of nature are the most important from an ecological point of view, but it has probably to pass through the laborious stage of physiological investigation of constant temperature in order to lay a foundation for the understanding of the varying conditions of nature.

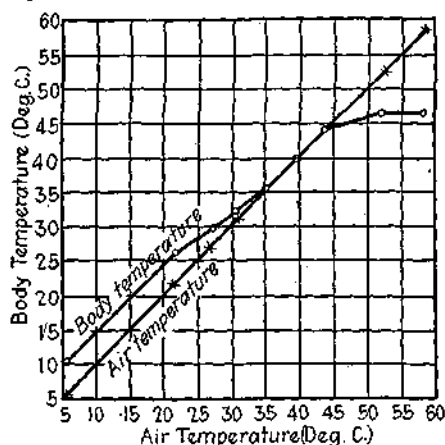


FIG. 22.—Graph showing the relation of body temperature of Italian bees with the surrounding air. (Pirsch, 1923.)

The Extremes of Temperature.

Attention has already been called to the fact that the rates of biological processes are slowed down as temperatures approach the extreme. This slowing down is much more noticeable and much more gradual as the low temperature is approached, and is so rapid at the higher temperature that it is hardly noticeable, the organism passing from a rapid rate to a secession of development very quickly. Lists of extremes of temperature which various insects have been known to endure have been published by Bachmetjew

(1907), Davenport (1908), Folsom (1922), and others. The absolute maximum temperature is in general in the region of 48°C. There is seemingly less variation in the absolute maximum temperature among the various species than in the absolute minimum temperature. Presumably the coagulation of protein is involved in death at the high temperatures. Pirsch (1923) found that honey bees seemed to be able to depress their temperatures slightly at very high temperatures (Fig. 22). This depression is due presumably to evaporation and can be maintained for only a very short period of time and only through the range of a few degrees centigrade.

Chapman, Parker, Mickel, and others (1926) found that there was not necessarily a correlation between the absolute maximum temperature which an insect might endure, and the environment in which it lives. The *Bembix* wasps, some of the predominant species of the sand dune, are not able to endure high temperatures. They escape them through

their behavior by alternately digging for a few seconds on the surface of the hot sand and flying about rapidly a few inches above, where the air temperature is considerably lower. It was found that species from the forest had neither the ability to endure the high temperature nor the protective reaction to avoid it. Reaction to avoid high temperature is much more certain than reaction to avoid low temperature, for activity is usually rapid and the organism can act to escape the extremes. But at low temperatures, where activities are already greatly slowed, reaction may be very sluggish and very indefinite.

Johnson (1895) cites the example of a Stratiomyid larva found in a hot spring by Bruner supposedly at 69°C. It seems uncertain as to whether the larva was actually at this temperature, which is 20° higher than would be expected. Brues (1928) made a study of the fauna of the hot springs of the Western United States, and found that the flies (*Diptera*) and the beetles (*Coleoptera*) were very abundant. Among the *Diptera* he found one species of *Stratiomyidae* (*Odontomyia*) at a temperature between 49 and 50°C. Table V shows the general results of the stratiomyid family in general, and it will be seen that they range from 28 to 50°C. In the case of these thermophilous insects, there can be no doubt that they endure the temperature of the water which surrounds them, for there is no known mechanism for their depressing their temperature below that of the surrounding medium. The tempera-

tures endured by the beetles go through almost the same range. Figure 23 shows the distribution of species as Brues found them in hot springs. It will be noticed that relatively few of them are able to endure temperatures as high as 45 and 46°. Only five species were taken in water above

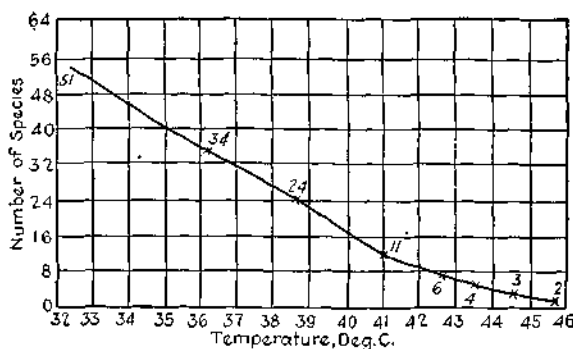


FIG. 23.—Graph illustrating the number of species of water beetles collected in hot springs at temperatures from 32° to 46°C.

40°C. Brues states that probably no beetles are reported to have been found in water the temperature of which is higher than 46°, except some reported in records which are possibly slightly in error.

Graham (1922) found certain buprestid larvae living under bark at a temperature of 52°C., and found also that a large percentage of larvae at the higher temperatures under bark were killed. It would be possible to continue to cite records of high temperatures which have been endured by insects; but it seems sufficient to call attention

TABLE V.—TEMPERATURE, SPECIFIC GRAVITY AND pH OF WATER WHEN CERTAIN DIPTEROUS LARVAE WERE FOUND¹

Hot spring, No.	Temperature, °C.	S. G.	pH	Name
1	38.7	1.0030	8.1	Odontomyia sp. No. 1
4	39-46.7	1.0212	8.3	Odontomyia sp. No. 2
5	35	1.0012	8.5	Stratiomyia No. 1
8	33	1.0030	8.0	Odontomyia No. 4
10	43-47	1.0014	7.3	Odontomyia No. 5
10	43-47	1.0014	7.3	Stratiomyia No. 2
10	43-47	1.0014	7.3	Oxycera sp.
10	43-47	1.0014	7.3	Nemotelus sp.
11	30-40	1.0016	5.7-6.5	Stratiomyia No. 1
13	28	1.0021	6.7	Stratiomyia No. 1
18	49-50	1.0008	8.1	Odontomyia No. 3
20	38	1.0014	8.6	Odontomyia No. 4
22	38	1.0014	7.8	Odontomyia No. 2
22	38	1.0014	7.8	Odontomyia No. 4

¹ BRUES, 1928.

to the fact that the general range of high temperature which may be endured by insects is rather constant, 48 to 52°C. being the absolute limit of authentic record. The organisms which live in environments of unusually high temperature may have a slightly higher maximum

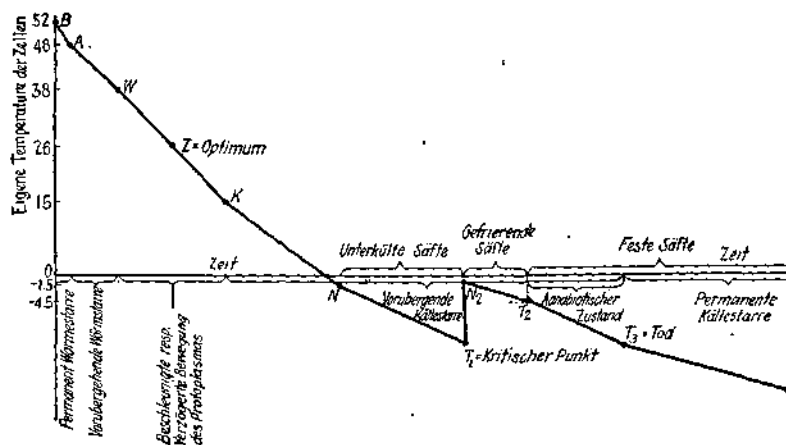


FIG. 24.—Bachmetjew's illustration of the effect of temperature upon protoplasm. (Bachmetjew, 1901.)

effective temperature, and they must have a very precise reaction to high temperature in order to avoid the conditions which would bring about death.

The effects of low extremes of temperature have received more consideration from investigators than have the effects of high extremes.

Bachmetjew (1901) made rather extensive investigations and summarized the early literature on the subject. His classical diagram (Fig. 24) illustrates his conception of the action of low temperature. Temperature is indicated on the vertical axis; and time, as involved in the lowering of temperature, is indicated on the horizontal axis. The insect may be cooled below the freezing point without being injured. The freezing point may be past, and the insect may exist in an undercooled condition. When it does freeze, the heat of crystallization will be equal to the undercooling temperature, and the body temperature will rebound to the freezing point. Cooling will again proceed; and when the insect reaches the undercooling point the second time, death follows, according to Bachmetjew's conception.

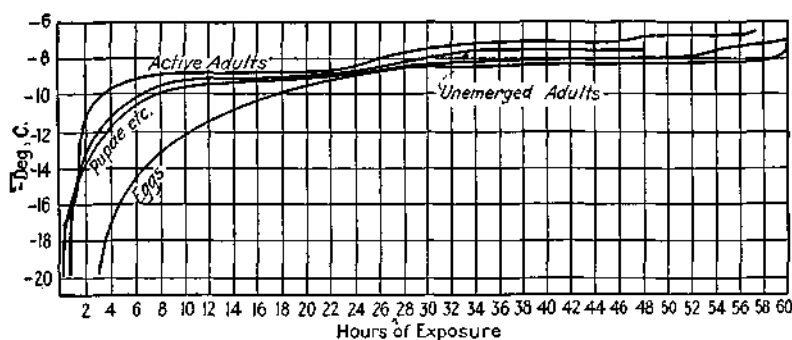


FIG. 25.—Fatal time-temperature for all stages of the life cycle of *Bruchus obtectus* Say (Carter, 1925.)

The more recent contributions to our knowledge of the ability of insects to endure low temperatures tend to indicate that not only temperature but moisture is involved. The subject becomes highly technical, and for the most part is of purely physiological interest. It will be referred to here briefly, and taken up more fully under the heading of Dormancy.

It may aid somewhat in understanding the effects of low temperature, if we distinguish between the intensity factor and the capacity factor. Some organisms are able to endure a temperature at which they become dormant, but are not able to endure it for a long period of time. Others are able to endure a low temperature for a short period of time, but do not have the capacity to endure such low temperatures over a long period. Some organisms die if they become dormant for a long period; others are able to endure low temperatures so long as they do not freeze. Freezing, however, is fatal to them. Still others are able to endure freezing, and may continue in this state for a long period of time. It would seem, in general, that the tropical insects, including those of tropical origin, do not have the capacity for enduring dormancy. This is true of *Tribolium confusum*, which will die in a few weeks at 7°C.

Carter (1925) made a study of the effects of low temperature upon the bean weevil in all the various stages of its development. The general results are indicated in Fig. 25. This graph shows the correlation between the temperature and the time involved in killing. Carter concluded that none of the stages could endure temperature of more than -19° for longer than a few hours' time.

Payne (1926) got evidence that certain insects which are normally exposed to extremes of temperature undergo a hardening during the fall of the year, during which time their freezing points are depressed and their ability to endure cold is increased. In the spring the reverse of this process occurs. She also found that the highest-per cent of larvae killed in nature occurred in the spring, when cold spells were experienced after the freezing point, and endurance of low temperature had been altered. This seems to indicate that, while the endurance of freezing may be a purely physiological question, it is of importance in ecology, in that the per cent being killed in out-of-door conditions depends upon whether or not they are able to endure freezing and just what physiological condition obtains at the time that they are exposed to low temperature.

Robinson (1928) has given a detailed account of the method of determining freezing points. He has shown that the temperature taken by piercing an insect with a thermocouple is not the true freezing-point temperature of the insect. He devised a method whereby the external temperature is taken, and the internal temperature is calculated from a correlation chart. Figure 26 shows Robinson's thermojunction and insect holder for taking the contact temperatures by the use of the thermocouple and pyrovolter, or potentiometer. In Fig. 27 the correlation is shown between the actual contact temperature as read and the internal temperature of the insect. The correlation chart is made by connecting the insect with an internal and external thermocouple junction. The insect is then placed in the constant-temperature cabinet, and the internal and external temperatures read at a series of constant low temperatures. After this chart has once been made up, it is possible, in the study of the same species, to read the external temperature and calculate the internal temperature from the chart.

Robinson (1927) found that the pupae of the promethea moth, which are exposed to low temperature in nature, may be frozen and endure dormancy in this frozen condition for months, since they are able to endure a temperature of -35°C. and survive.

A provisional generalization may therefore be made, that tropical insects which are not normally exposed to extremely low temperatures are unable to endure dormancy. In general, insects of temperate regions, which hibernate in exposed conditions, are able to endure freezing and survive; and such other insects as migrate into the soil, or

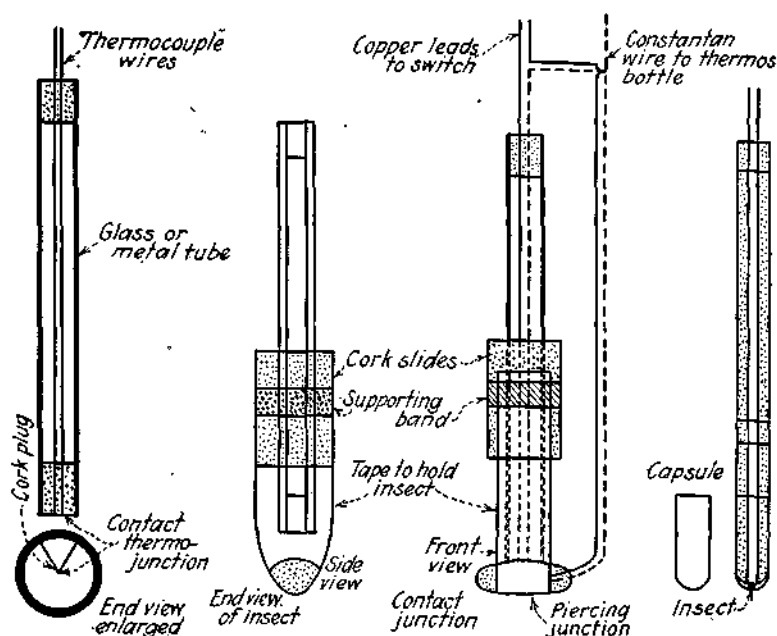


FIG. 26.—A thermojunction with insect holder for use in making contact-temperature determinations. (Robinson, 1928.)

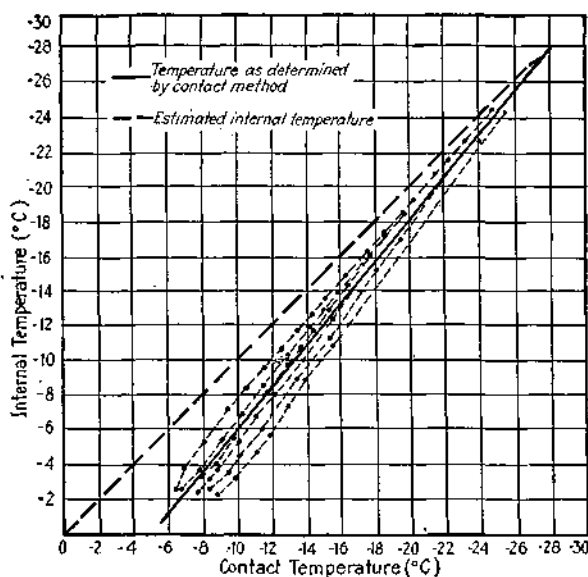


FIG. 27.—A correlation chart to be used in determining the actual internal temperature of an insect from its surface temperature as recorded by contact. (Robinson, 1928.)

in other ways provide themselves with protection against freezing temperatures, are able to endure dormancy, but are unable to endure freezing. The subject of Dormancy will be found in a discussion under that heading.

Effects of Temperature on the Morphology of Animals.—The effect of temperature as an environmental factor upon the morphology, the structure, and the color of organisms is, in part, a purely physiological consideration; but it is also of ecological importance, in that the resulting organism may be considered as characteristic of a definite environmental condition. In general, the information which we have of the effects of temperature upon the morphology of organisms may be placed in two classes: one, the information which has come from systematists, who have observed that the representatives of a species which come from one extreme of the range of the species differ morphologically from those which come from the other extreme of the range. If the extremes involved are the Tropics and the Arctics, it is usually assumed that the differences are due to the effect of temperature. Bachmetjew (1907) cites many instances which undoubtedly belong to this class of information. No doubt many of these conclusions are well founded, but it is difficult to evaluate them in the absence of direct observations. In the second class of information we have that which comes to us from direct observations made under more or less controlled conditions. It is possible to subdivide this information into that in which the correlation of temperature with the morphological change seems apparent although there is no explanation of the mechanism involved, and that in which the effect of temperature has been studied and a mechanism found which seems to account for the morphological changes.

Literature contains a great deal of information with regard to the effects of temperature; these records may fall into any of the three classes just described. It is not the present purpose to tabulate all these cases and to classify them, nor is it the purpose of this volume to discuss in detail the subject of "Entwicklungsmechanik." A few of the apparently authentic cases will be described with the hope that it will lead to a better understanding of the action of temperature upon form and structure, and that it may also stimulate further investigation in this very interesting field.

The Effect on Form and Structure.—The effect of temperature upon the form and structure of an organism may arise from a differential effect of temperature upon the several contemporaneous processes which are going on during the development of the organism, resulting in a greater acceleration of some processes and an inhibition of certain other processes.

Hegner (1919) reports that the spines of the protozoan *Arcella* are longer when developed at high temperature than at low temperature.

There may even be some ecological significance in this condition, for the viscosity of water and consequently its buoying effect in supporting such a protozoan is reduced at high temperature, but the increase in the surface of the organism from a longer spine will result in a greater ability of the organism to float. However, the particular point of interest here is Hegner's statement that the spines are longer when the organisms are developed at high temperature than when they are developed at low temperature.

Another case is reported by Roberts (1918), who states that a difference of 4 or 5°C. gave longer wings in the mutant form of *Drosophila*, which is called vestigial, than did 29 generations of selective mating. This mutant race of *Drosophila* has small wings. The length of the wings varies, but they are always small. The variation of these short wings is effected by temperature, and the difference of temperature of 4 or 5°, as just stated, gives longer wings than 29 generations of selective mating.

Gerould (1924) reports that he was able to reduce the size of the wing of *Colias* by rearing it at low temperature. This seems to be consistent with the other literature which has just been cited.

If we are to turn our attention to some of the older experiments, we shall find a long series of papers by Standfuss, Merrifield, and others on the effect of temperature upon various lepidoptera. Bachmetjew (1907) summarized these results in which various stages of *Vanessa urtica* were subjected to various temperatures. The adults resulting from exposures to low temperature were like the small variety *polaris* of Lapland; while those which developed at high temperatures gave rise to large adults similar to the variety *ichmuse* of Sardinia. This is not cited as an example of the inheritance of an acquired character; it is simply cited as an example of an organism which is so affected by low temperature that it appears like the individuals which live in the northern regions, or when subjected to a high temperature the resulting adults appear like those of the southern range of the species. The northern ones are small, which is consistent with the results of Gerould (1924), and they are darker in color than the southern ones.

Kühn (1926) found that there were four fundamental pattern systems which behaved more or less independently in *Vanessa*, and were effected by subjecting the pupae to low temperature. The period of maximum sensitivity for the hind wing was 12 to 36 hours after pupation; and for the fore wing, 24 to 36 hours after pupation.

There are many other cases which may logically belong under the effect of temperature on the mechanism of heredity though it seems probable that it is difficult to make a distinction between the effect of temperature upon the mechanism of heredity and the effect of temperature upon the processes of development, as we normally think of

them in ontogeny. Possibly the fundamental nature of the effect is much the same regardless of whether it takes place during the process of chromosome arrangement, or later when cells are proliferating. For the sake of convenience, the cases which seem to be concerned with the mechanism of heredity as such will be considered under that heading.

24 **Effect on Color.**—What has been said with regard to the effect of temperature upon morphology in general might be repeated with regard to the effect of temperature upon color, in that the literature on this subject is very voluminous and much of it consists of superficial correlations of temperature and color. There are, however, certain pieces of careful experimental work which seem to indicate very definitely not only that color is affected by temperature, but that there is a mechanism which is affected by temperature and which determines the color. It will be quite impossible to attempt to evaluate all the various evidence which has been published as to the effect of temperature upon color. A few examples will be selected in the hope that they may show rather definitely how temperature may act in this way.

✓ Knight (1924) investigated the color pattern of *Perillus bioculatus*, which had been observed under field conditions to be black and white during hot dry periods, and red and black during cooler periods of the year. In this case the white tended to be replaced by yellow and red; and the black portions of the pattern, to be more extensive at the low temperature. Under experimental conditions, nymphs were reared through to the adult stage at high temperatures, and gave the white-marked adults. When nymphs were reared through at low temperatures, the patterns were dark. When adults of a light color pattern were placed at a low temperature, they began to show the yellow and red coloration. An investigation of this pigment has shown that in this case it is carotin, and that the blood of the potato beetle larva, on which *Perillus* feeds, is saturated with this pigment. The potato beetle gets the pigment from the potato plant, which probably synthesizes it. *Perillus* then obtains this pigment in its food. When metabolism is going on rapidly at high temperatures, the pigment is oxidized. At low temperatures the oxidation is less rapid; and some, at least, of the pigment is deposited in the hypodermis of the insect and thus appears in its patterns, giving a light-yellow to a dark-red color, depending upon how much has been deposited. When this pigment is deposited in the hypodermis of the body wall of adult bugs, it is permanently placed and is not oxidized later even at high temperatures. Knight concludes:

In the case of *Perillus* then, it appears that the physiological activity of the insect which is modified by the temperature is oxidation, influenced by the physical activity of the insect, and that this is the fundamental explanation of the pigment variations.

The black color of *Perillus* is also influenced by temperature, being more abundant at the lower temperature. Knight concluded that this was melanin, as was found by Gortner in 1911, and that it was deposited in the cuticula.

Toumanoff (1926) studied the effect of temperature and darkness on the melanism of *Dixippus morosus*, and found melanism developed at high temperature and inhibited at low temperature. Toumanoff concluded that the lack of melanism at low temperature might be due to several things: a diminution of the absorption of oxygen necessary for the reaction at the low temperature; or perhaps a general effect upon metabolism which failed to produce the necessary polypeptid and tyrosin, which constitute the chromogen; or the fact that the low temperature affects the action of oxidase and tyrosinase, which are involved in the development of the melanin.

Gerould (1924) states that he has found that the amount of melanin in the markings of the butterfly, *Colias*, varies inversely with the temperature. He does not seem to distinguish between the formation of the pigment and its deposition. He states that any factor which will interfere with the reaction of tyrosin, tyrosinase, and oxygen will interfere with the formation of the pigment melanin. From this statement it seems difficult to understand how low temperature would increase the amount of melanin formed and thereby give darker color at lower temperature, as Gerould states that it does.

Schlottke (1926) found that the pigment which develops at the points of attachment of the muscles in the parasitic wasp, *Habrobracon*, bears a linear relationship to temperature. There is less pigment at high temperature than at low temperature. When they are reared at first at low temperature and then raised to high temperature, they become lighter than those which are reared constantly at high temperature.

The Effect of Temperature on the Mechanism of Heredity.—Environment and heredity have been looked upon as two opposing forces in nature, ever since the stability of the species was demonstrated. When some of the first laws of heredity were definitely outlined and the evidence in their support was being amassed, it was the opinion of many biologists that the characteristics of organisms were determined by heredity and that environment was in no way able to influence them. We now have a much better conception of these two factors in determining the structure of an organism. Weinstein's statement has already been quoted; to the effect that it is no more possible to state that the characteristics of an organism are more dependent upon heredity than environment, than it is to state that the area of a rectangle is more dependent upon its altitude than its base.

We are now in a position to consider the effect of temperature upon the mechanism of heredity in much the same way that we would consider

its effect upon any other physical or biotic phenomenon. It may be possible to differentiate between (a) the effects of temperature upon the position of genes and the behavior of the chromosomes, and (b) the effect upon the processes of development which go on after the cells have been fertilized and have started their development, in differentiating the various organs of the animal. We may again turn to the monumental work of Bachmetjew in summing up the early literature on temperature and heredity. It is to be noticed that the "object" of much of the early work was to produce new species through the effect of temperature. The interest here will be in trying to find a correct interpretation of the effect of temperature upon the mechanism of heredity and thereby upon the organisms which live under various environmental conditions.

Seiler (1920) reported that extreme heat caused the sex chromosomes of *Taleporia tubulosa* to remain in the egg at the time of reduction division, thus increasing the number of potential females.

Mann (1924) made a study of the stability of genes, and used high temperature in a series of experiments. It was found that the percentage of males was increased at high temperature, such as 31.5°C.; but that the percentage was decreased when the progeny were again returned to a temperature of 25°C. There is no implication in this case that the effect produced would be operative beyond the individuals which were developed from the germ cells which had been exposed to this high temperature.

Plough (1917) studied the effect of temperature on the phenomenon of crossing over in *Drosophila*. It does not seem difficult to conceive of a possible effect of temperature upon such a phenomenon as crossing over, for the chromosomes must obey the physical laws which have to do with their movement during the various processes involved in maturation division. It seems logical that certain environmental factors might affect the rate and extent of the movement of the chromosomes during mitosis; and temperature is certainly a factor which might do this through viscosity, surface tension, and various other physical phenomena. Plough found that the extent of crossing over was increased at high and at low temperature, and that a minimum amount of crossing over took place during a range of temperature between about 20 and 27°. The general results of his investigation are shown in Fig. 28. This is a case in which hereditary characters might appear to be greatly affected by the environmental conditions having to do with different temperatures.

It has recently been found that mutations, which presumably occur in nature as rare but normal accidents, may occur more frequently under certain temperature conditions. Geneticists seem inclined to look upon mutation as the most important phenomenon in nature concerned with the change in the genetic constitution of an organism. If this proposition is accepted and the work which has been referred to is substantiated,

we then have an example of temperature affecting the hereditary constitution of an organism in a most profound way.

Hersh (1924b) observed the effect of temperature upon the dominance of one character over another.

In some cases dominance seemed to be influenced by temperature, while in other cases it was not influenced at all. In a heterozygous stock of *Drosophila* with various eye characteristics, 27°C. seemed to be a critical temperature for change in dominance. Zeleny and his students have made a thorough study of the eye of *Drosophila* as affected by heredity and certain environmental conditions.

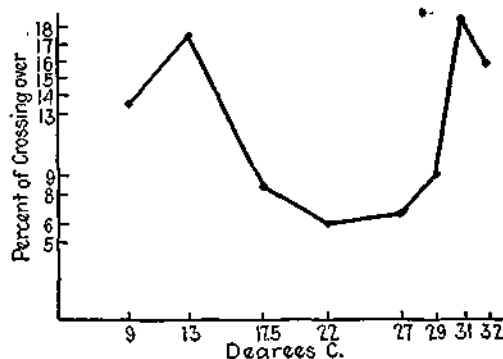


FIG. 28.—The effect of temperature on crossing over in *Drosophila*. (Plough, 1917.)

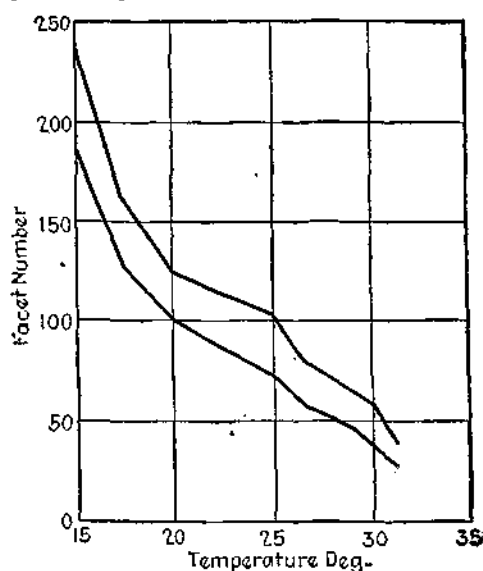


FIG. 29.—Temperature effect on the facet number in low selected bar stock of *Drosophila*. Upper curve for males, lower curve for females. (Krafka, 1920.)

Krafka (1920) investigated the effect of temperature on certain "mutants" of *Drosophila* which have a small number of facets in the eye and are termed "bar-eye." He also had another strain known as ultra bar-eye. He found a linear relationship between the number of eye facets and the temperature under which the flies were reared, the mean facet numbers varying from about 28 at 31°C. to 189 at 15°C. In the ultra bar stock the same linear relationship obtained; but the numbers were lower, being about 14.57 for the mean facet number at 31°C., and 51.51 at 15°C. (See Figs. 29 and 30 for the distribution of

facet numbers.) When these results are compared with those of Hersh (1924), an interesting comparison may be made between the normal full-eyed *Drosophila*, the mutant bar-eye, and ultra bar-eye. In the normal full-eyed *Drosophila*, Hersh found that there was nearly a straight-line relationship between temperature and number of facets. Above

27°C. the change in facet number was much less, and the result deviated

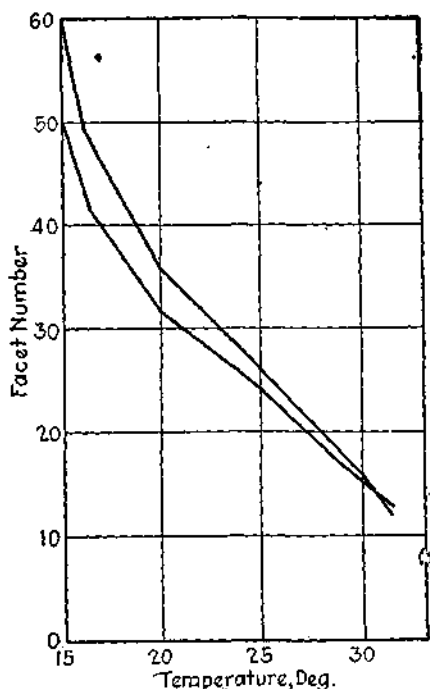


FIG. 30.—Temperature effect on the mean facet number in the ultra-bar stock of *Drosophila*. Upper curve for males, lower curve for females. (Krafka, 1920.)

from the straight line (see Fig. 31.) The normal full-eyed *Drosophila* varies from between 900 and 1,000 facets at 15°C. to about 700 at 27°C. The largest number of facets which may be produced in the so-called "mutant" bar-eye at low temperature is much less than the lowest number produced in the full-eyed *Drosophila* at high temperature. In comparing the bar-eye and the ultra bar-eye, however, it is found that there is an overlapping in the mean facet numbers, for as many as 51.51 may be produced at 15° in the ultra bar-eye, and as few as 28.85 at 31° in the bar-eye. The result is that we have two genetically distinct strains which can be made alike, as to the mean facet number, by rearing one at a low temperature and the other at a high temperature. Under the conditions of nature, these two strains might well be confused on the basis of mean facet number.

There would, however, be no possibility of confusing the mutant with the

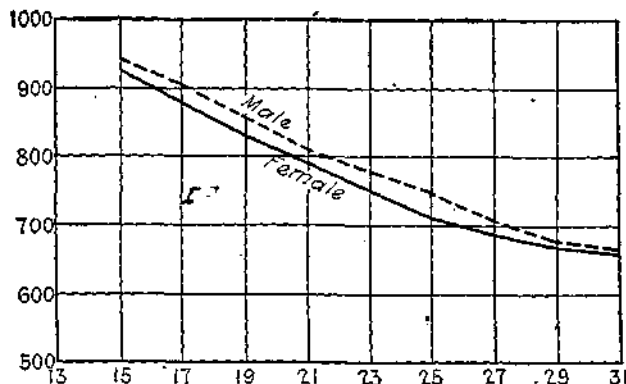


FIG. 31.—Mean facet values in full-eyed *Drosophila* plotted in terms of temperature. (Hersh, 1924.)

normal full-eyed *Drosophila*; for the fewest facets that can be produced by high temperature in the normal full-eyed *Drosophila* is far greater than the highest number in the bar-eyed *Drosophila*.

Krafka believes that the linear nature of the relationship between the eye-facet number and the temperature indicates that it is a result of a differential effect of temperature on the processes concerned with the development of the eye facets as compared with the rest of the individual. He also found that the effect of temperature in determining the number of eye facets is operative during a rather restricted period. At 27°C. this period is said to occur between the end of the third and the end of the fourth day, and to have a duration of about 18 hours. At 15°C. this period is at the end of the eighth day following a first day at 27°C. In this case the period is 72 hours long. Krafka examined a number of hypotheses, in the light of the data at hand, without being able to demonstrate definitely what the nature of the process which causes the change in facet number might be. It seems certain that this is of the nature of the effect of temperature on development rather than of the mechanism of heredity.

Zeleny (1928) reports that this culture of *Drosophila* has been continued over a long period of time without any definite effects upon the inheritance of the character.

There are other examples of the effect of temperature upon the size and length of the wings of *Drosophila* (Nadler, 1927), and of other factors on other species, which show that temperature may affect the mechanism of development in such a way as to give rise to individuals having a definite correlation between the temperature and the characters developed.

Effect of Temperature on the Behavior of ^{animals} Animals.—Changes in temperature constitute stimuli to which animals react, as in the case of other physical factors of the environment, to choose an optimum condition. This reaction is well known in the case of temperature, and will not be considered further except as an illustration of the effect of temperature upon reactions of poikilothermic animals.

The mechanisms by which poikilothermic animals react to unfavorable temperatures are themselves affected by the temperatures. Consequently, when such an animal encounters an unfavorably low temperature, its movements will be slowed and its reaction in avoiding this low temperature will be retarded. If the temperature is very low, the animal may become torpid before the reaction is complete. In the case of an unfavorably high temperature, the movements will be very rapid and the avoiding reaction accelerated, unless the temperature is so extreme that it produces a depressing effect.

The universal effect of temperature upon biotic processes extends to the effect of temperature upon the reactions of animals to all sorts of stimuli. It is necessary to interpret the reaction of animals to any stimulus in terms of the temperature under which the reaction is brought about. Consequently, certain animals may be positive to one stimulus

at one temperature and negative to the same stimulus at a different temperature. The change of certain animals in their reactions to light is a classical example of this temperature effect. Many animals are negative to light at low temperature, and positive at high temperature. This effect of temperature is undoubtedly an important factor in controlling the complex system of stimuli and reactions which govern the diurnal activity of animals.

An interesting example of the reaction of an insect to the diurnal changes of temperature is furnished by a leaf-mining beetle, *Taphrocercus gracilis*, belonging to the family *Buprestidae* (Chapman, 1923). In the field it was observed that at high temperatures the adult beetles were positive to light and reacted by flying when stimulated mechanically. At low temperatures they were negative to light and contracted their appendages and permitted themselves to fall when stimulated mechanically. Inasmuch as the beetles retired to the axils of the leaves at low temperatures, their falling at this time merely resulted in their coming to rest in crevices in the axils of the leaves. Such a reaction at high temperature while they were feeding near the ends of the leaves would result in their falling into the water in which their host plant grows. At high temperature they are positive to light and react to mechanical stimuli by flying. Consequently, when feeding on the tips of the leaves they fly when mechanically stimulated, and do not fall into the water.

Observations on these beetles during the diurnal cycle of their activity indicated that the change of temperature had a profound influence upon all of their activities. Under controlled laboratory conditions they could be brought out of their retirement into the light by raising the temperature, and returned to their hiding places by lowering the temperature. It is known that the time of flight, feeding reaction, oviposition, and many other functions are controlled by the temperature in the diurnal cycle.

Effects of Temperature on the Geographic Range of Animals.—This subject is referred to in this place merely for the purpose of completeness of the discussion on temperature. It will later be referred to under the subject of the distribution of animals as correlated with climatic influences. The obviousness of the effect of temperature upon the geographic range of animals called early attention to this subject. Many investigators attempted to mark out zones of animal distribution on the basis of temperature alone, neglecting all other factors.

Merriam (1894) based his "life zones" on his so-called "laws of temperature control." He stated: "Animals are restricted in their northern distribution by the total quantity of heat during the season of their growth and reproduction," and "Animals are restricted in their southern range by the mean temperature of a brief period during the hottest part of the year."

These statements imply that animals may live as far north as the season will permit sufficient units of time and temperature for the completion of the cycle. It neglects the fact that animals are often limited in their northern distribution by the extremes of temperature during the winter. Most of this work has been based upon a summation of time and time temperature above some assumed minimum effective degree of temperature. The zones of Merriam were thus based upon a summation of temperature. Merriam states that the temperature sums which he gives as characteristic of the various zones were obtained by summing the temperatures above 43°F. from spring to fall and that the conversion from centigrade to Fahrenheit was made. Such procedure does not give his results. He summed the total number of degrees Fahrenheit for each day from spring to fall, starting with the first day above 43°F. The conversion was made from Fahrenheit to centigrade, but no account was taken of the fact that "0" in the Fahrenheit scale is 32°F. lower than on the centigrade scale. Consequently, all of his values given in degrees centigrade are incorrect.

Bodenheimer (1927) made a study of two weevils, *Sitophilus oryza* and *Sitophilus granaria*. He calculated the constant for time and temperature for *S. oryza* as 358.8, and for *S. granaria* as 523. It does not follow, however, that *oryza* is to be found in the North, and *granaria* in the South. It is just the opposite, even though *oryza* requires the lower number and *granaria* the higher number of day degrees. The curves of development when plotted as time and degrees cross near the middle, so that *oryza* develops relatively more rapidly at high temperatures, and *granaria* more rapidly at low temperatures. Consequently, *Sitophilus granaria* is the northern species; and *Sitophilus oryza*, the southern species. This is in conformity with the actual conditions; but it could not be deduced on the basis of the sum of time and time temperature required for the completion of the life cycle.

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CHAPTER IV

MOISTURE AS AN ECOLOGICAL FACTOR

Introduction.—(There is no other substance which contributes so largely to the structure of organisms as water does.) It is the general presumption that life was originally aquatic, and it is true that organisms have never entirely freed themselves from an environment which must contain a certain amount of water. (One of the fundamental necessities for all organisms is to maintain a certain balance between the moisture in their bodies and the moisture in the surrounding environment.) (The amount of moisture contained in the bodies of various species of organisms varies greatly. Some of the aquatic organisms have only a fraction of 1 per cent of substances in addition to the water of their bodies. Amphibious organisms are able to endure the greatest fluctuations in the moisture content of their bodies. Xerophytic animals may be adjusted to very low moisture content) but in general in such cases the variation in the moisture content cannot be great. In terrestrial environments the variation of moisture in geographic range is very marked and is one of the outstanding factors in controlling animal distribution. The distribution of moisture in the annual cycle is usually very marked, and serves as an easy method of distinguishing between the various types of environment.

Characteristics of Moisture as an Ecological Factor.—(Moisture as an ecological factor differs from the two which we have just considered, in that light and heat were forms of energy which are made use of by animals, but moisture is a medium in which all organisms live.) It may be so concentrated as to constitute an aquatic environment, or be so dilute as to be characterized as an arid desert; but it must, nevertheless, be present as an essential part of the environmental medium. (All food which the organisms take into their bodies must contain at least a minimum amount of water present as such, or potentially present in the compounds which are to be broken down by the animal's metabolism.)

(Moisture may be present as a solid, liquid, or vapor. But organisms are concerned with it chiefly as liquid and vapor.) The ever-recurring cycle from liquid to vapor and from vapor to liquid is of fundamental importance, whether considered in its largest sense as a balance between the water and water vapor of the entire earth; as precipitation and evaporation over given areas; as the great series of cycles within cycles which involve the metabolism of organisms and the maintenance of a balance between the intake and loss of water; or even down to the individual cells of the organisms. In all of these exchanges, an equilibrium

between the two phases of liquid and vapor must be maintained. (For the environment, the ratio between precipitation and evaporation is important. For the individual organism, the ratio between moisture intake and moisture loss is of great importance.) The problems involved in these cycles extend from those of purely physiological interest, involving the water films on colloidal particles within the cells, to the action of water as an agent in erosion as concerned with problems of geology and physiography. In this great range there is much of direct concern to the ecologist.

Methods of Measuring Moisture.—When attention is turned to the measurement of moisture as an ecological factor, it must first of all be realized that there are several phases of this factor which may be measured. We may distinguish first of all between the measurement of the state of moisture which may include the moisture content of the medium, whether it is air in which it is expressed as humidity, or whether it is a solid medium, such as soil; or a nutrient medium, in which it may be measured and expressed as per cent of weight or volume. The alternative is to measure the rate of change from one phase to another, in which case we may measure precipitation and evaporation. All of these measurements are important, and the ones which are to be taken depend very largely upon the type of problem in which the ecologist happens to be interested. For convenience we shall take up first the measurement of the state of moisture, and later the measurement of the change in phase of moisture.

(The state of moisture in the air is usually expressed in relative humidity, in whatever way the reading may be made. The relative humidity is the amount of moisture present in a space as compared with the amount required to produce a condition of saturation at the same temperature and atmospheric pressure.) (It is expressed as per cent of saturation, and is an important expression because it represents the state of equilibrium of the atmosphere in the moisture cycle.) (The absolute humidity is the amount of moisture by weight in a given volume of space.) In the English system this is expressed as the number of grains of moisture per cubic foot. Or (it may also be expressed as grams per cubic meter.) The expression of absolute moisture is very definite; but its determination is difficult, and it does not take into consideration conditions under which the moisture is present in the space. Consequently, (relative humidity is much more significant than absolute humidity.)

Marvin (1915) gives a good description of the method of determining the relative humidity of the air. Bongards (1926) gives a thorough discussion of the theory of gases and vapors as well as the methods and instruments involved in measuring and recording humidity. Carrier (1911) and Shelford (1929) may also be consulted.

(The relative humidity of a space may be determined: (1) by ascertaining the dew point, (2) by the wet-bulb depression on a wet-and-dry bulb thermometer, (3) by some type of hygrometer which may involve chemical solutions or the hygroscopic coefficient of some material which is commonly hair. The psychrometer, which involves the principle of the wet-and-dry bulb thermometer, is the most common instrument used. The United States Weather Bureau uses a sling psychrometer, which consists of two standardized thermometers mounted side by side, one with the bulb projecting below that of the other. This bulb is covered by a wick, which may consist of silk or muslin. The wick is moistened with distilled water, and the psychrometer is then whirled through the air to give a uniform rate of air movement over the wet bulb. This is essential to produce evaporation at a given rate. The psychrometer is whirled through the air and read at intervals to determine the lowest point of the wet bulb. When this is past, the temperature of the wet bulb begins to rise, and the operator knows that he has obtained the lowest depression. The difference between the wet and the dry bulbs is then read and referred to a table which has been prepared by the Weather Bureau on the basis of a series of experiments under various conditions of humidity and pressure. Several types of tables and graphs are now available. They usually involve the readings of the dry bulbs and the depression of the wet bulbs, and from these the relative humidity may be taken.

Such a psychrometer is not convenient to use in a small space. Therefore, various types of cog psychrometers have been made. These consist essentially of mounting two thermometers in either an egg-beater or a cream-whip mechanism, so that they are whirled through a small circle by a mechanical means.) Gray (1929) has described a convenient form of cog psychrometer (Fig. 32).

The dew-point determination is probably the most dependable for use in small spaces. Marvin (1915) and Shelford (1929) described mechanisms for making this determination. A small silver tube can be mounted in a test-tube clamp and filled with ether. A thermometer is then mounted in the ether, and air is aspirated through to lower the temperature by evaporation. It is necessary to observe very carefully and to lower the temperature on a very slow gradient in order to note the first appearance of moisture deposited on the surface of the silver tube. The temperature then must be read accurately. The relative humidity may be determined from tables which may be found in Marvin (1915), "International Critical Tables," Vol. I, and various other books of physical and chemical constants. It is necessary to read the dry-bulb temperature at the same time that the dew-point temperature is read.

(Holtzmann (1924) devised a simple mechanism for determining the dew point in small spaces. It consists essentially of a silvered rod of

metal of low heat conduction which is so maintained that one end can be warmed by a resistance coil, and the other end may be cooled by an evaporation mechanism. The instrument is mounted in such a way that it is possible to observe the metal rod, which has a line drawn around it near the middle; and in this line a thermocouple is mounted. The one end of the rod is cooled, and the point at the edge of the moisture which is being deposited moves slowly along toward the warmer end. Precisely as this mist reaches the line, the temperature is read by means

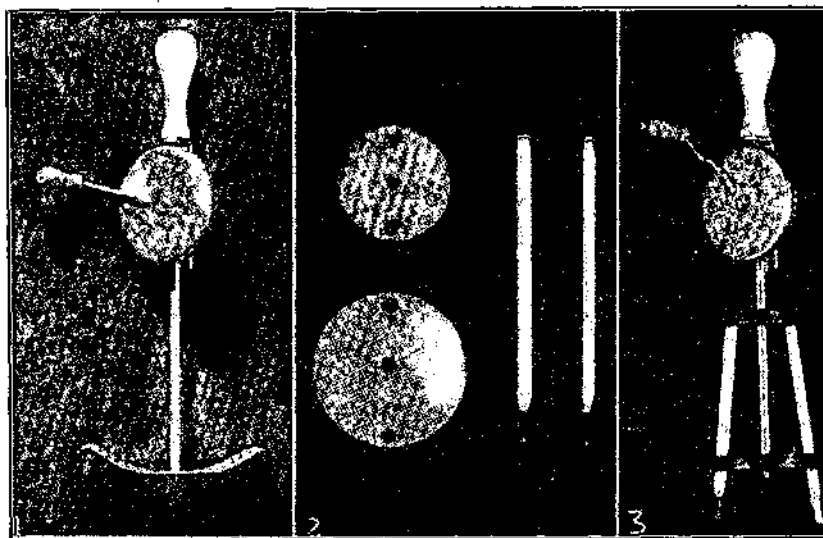


FIG. 32.—Cog psychrometer. The steps in making a readily available cream whipper into a psychrometer. 1. The cream whipper. 2. Thermometers and rubber disks ready to assemble. 3. Model completed and ready for operation. (Gray, 1929.)

of the thermocouple. The opposite end of the rod is then warmed and the area of mist is driven back toward the cool end. As this reaches the line the second time, the thermocouple is read again. The mean of the two readings gives a very accurate dew point. A mechanism of this type is useful in small breeding cages.)

(The hygrometer principle may also be made use of in small spaces. Commercial hygrometers usually consist of human hairs, the expansion and contraction of which is governed by their hygroscopic coefficient.) By consulting the "International Critical Tables" Vol. I, one will receive many suggestions as to materials which might possibly be used in hygrometers. The expansion and contraction of many of these materials show an almost straight-line relationship as compared with the temperature and the relative humidity of the air. (In the chemical hygrometers, sulphuric acid is the solution most commonly used.) Shelford (1929) gives certain details of this method.

(The moisture content of a medium other than air, such as food, soil, or wood, is usually stated in per cent of the total weight or per cent of dry weight, and is generally determined by evaporating a material to dryness. This may be done at a temperature of 105°C., and evaporation is usually continued until the curve of loss of weight flattens out.)

The per cent of moisture present does not necessarily give a significant indication of the state of moisture in a solid or semi-solid medium. In the case of soil, a measure of the availability of moisture for plants may be more significant than the actual content. The wilting coefficient of a plant is a biotic measure of the available water. The wilting coefficient of a soil is the moisture content of the soil, expressed in percentage of dry weight at the time when the leaves of a plant growing in that soil first undergo a permanent reduction in moisture content as a result of a deficiency in the soil-moisture supply. This wilting coefficient is nearly constant for any species.

A physical measure of the available moisture is expressed as the moisture equivalent, which is the per cent of moisture that a soil can retain in opposition to a centrifugal force equal to 1,000 times that of gravity. This is a convenient measure, since it has been shown to bear a straight-line relationship to the wilting coefficient.

Another physical measure is the hygroscopic coefficient. This is the moisture content of a soil when in equilibrium with a saturated air at 20°C. These measures all reflect the fact that water may be present in a medium as free water, capillary water, adsorbed on the surface of colloids, or combined in the various compounds. The significance of these physical states will be discussed in the chapters on Synecology.

Wilson (1921) also describes a method for determining the moisture equilibrium of a material by exposing it to a known vapor tension over a solution of sulphuric acid.

Zeleny (1909) devised a method of measuring the content of a material by the resistance offered by the material to the passage of an electric current. Robinson (1926) has modified this method to make it applicable to the determination of the free water in an insect and in certain other materials. The method is a delicate one and requires a considerable amount of apparatus for accurately determining the resistance to an electric current of about one volt with 1,000,000 ohms resistance. The more accurate determination of the amount of moisture present in a medium, which may be solid or liquid, is based upon the freezing-point depression. The literature of Robinson (1926), Bouyoucos (1921), and others is referred to for the technique for this method of determining moisture content.

(The change in state of the moisture is ordinarily measured in precipitation and evaporation. Precipitation is measured very simply by the use of cylinders, as described by Marvin (1903). These normally

stand vertically, and either may be straight cylinders, or at some point below the top may be narrowed down in diameter by a funnel in order to increase the depth of water. The ratio of increase of depth to the narrowing of the cylinder being known, it is possible to make a more accurate measurement of a small amount of precipitation. These normally are measured for 24-hour periods.)

(The evaporation which represents the change of water from liquid to vapor is one of the most important measurements of the moisture cycle, for all organisms are exposed to a certain amount of evaporation.) The rate of evaporation may be a measure of the temperature, vapor tension of the surrounding medium, the rate of air movement, and the barometric pressure. The following table from Shelford (1914) illustrates the influence of various factors on rate of evaporation.

TABLE VI.—A COMPARISON OF THE RATE OF FLOW AND EVAPORATING POWER OF THE AIR WHEN TEMPERATURE AND HUMIDITY ARE APPROXIMATELY CONSTANT¹

Approximate velocity, meters per second	Approximate evaporation, c.c. per hour	T.°C.	R. H. per cent	Increase in flow	Increase in evaporation
0.012	0.25	22.4	50	1	1.0
0.026	0.40	22.2	53	2	1.6
0.052	0.75	22.2	53	4	3.0
0.104	1.50	22.2	53	8	6.0
0.208	2.00	22.2	54	16	8.0
0.416	2.60	22.2	53	32	10.4

¹ SHELFORD, 1914.

(Evaporation may be read as the evaporation from a free surface of water of known area, or from a mechanism known as an evaporimeter. Evaporation from a free surface has a number of limitations, as accidents may happen to it in the field to affect the water level, and it is also difficult to measure accurately a water level and to maintain it in such a way that the rate of evaporation is not affected by the change in level. The most commonly accepted type of evaporimeter is the Livingston porous-cup atmometer (Livingston, 1908 and 1915). They are made as cones and as spheres. The spheres are the later type, which have uniform exposure to the sun's radiation; but unfortunately readings from spheres cannot be transformed into readings from cones. These atmometers are furnished standardized or unstandardized. The standardized ones are very desirable. They may be returned to the manufacturers and re-standardized at various periods. These are ordinarily mounted, so that it is possible to read the amount of water which has been evaporated directly from the jar containing the water.)

(Figure 33 shows the type which has been used in this laboratory at the University of Minnesota for reading evaporations over short periods

of time. There is simply a double connection to the atmometer, one connection leading only to a U-tube, which is graduated in one-hundredths of a cubic centimeter. The other connection, which leads directly

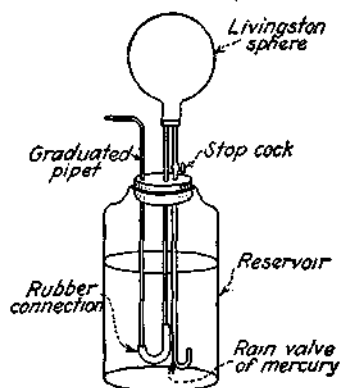


FIG. 33.—Graham's atmometer mounting for short-time readings of evaporation.

to the water reservoir, is provided with a cock, which makes it possible to shut off the source of water. To make a reading, the water is drawn up into the U-tube by suction, and the direct connection to the reservoir then closed off. The evaporation from the atmometer then proceeds directly from the calibrated U tube. When moved to a new atmosphere, such an atmometer must be permitted time to come into equilibrium. Thereafter accurate readings over a few minutes may be made with the aid of a stop watch.)

There are certain restrictions in the use of the Livingston atmometer. It can not be used below freezing temperature; and,

if exposed to rain, some valve must be introduced to prevent water from backing up into the reservoir.

Various mechanisms are described in the literature for checking the effect of rain. Nearly all of them have a slight coefficient, in that all mercury valves permit a slight displacement of the mercury when the suction on the atmometer is relieved by the rain. Graham devised a very simple method which has a small correction coefficient. It consists of a small bulb blown in one side of the J-shaped tube, which provides the water to the atmometer from the reservoir. A small drop of mercury is introduced into the tube; and, when the atmometer is drawing water, this mercury is lodged in the small bulb. When there is a back pressure due to rain, the mercury runs out into the J-tube and prevents water from returning to the reservoir.

Reinhard has devised an ingenious mounting, the description of which has not been published. It is shown in Fig. 34. In this case, the atmometer is mounted on a level with the water reservoir. The suction of the atmometer and the pressure of the water reservoir may be balanced by raising or lowering the air-supply tube. This atmometer has been operated under a water tap without any back pressure into the water reservoir. It must necessarily have a very rigid construction in order to prevent leakage at the joints.

Bates (1919) devised an evaprimeter constructed on much the same principle as that of a plant leaf. This was done because he felt that air

movement was too much of a factor in the rate of evaporation from a Livingston atmometer. Bates' evaporimeter consists of a horizontal disc mounted on a tube, through which a round wick leads up to a flat wick in the space between the upper and lower surfaces of the disc. The water is led up the round wick from the reservoir to the flat wick, from which it evaporates into the space in the disc. The aqueous vapor is diffused through holes in the lower surface of the disc much as it diffuses through the stomata of leaves.

The upper surface of the disc is polished to reflect the sun's rays and thus prevent insolation from becoming too strong an influence. The Bates evaporimeter is said to be capable of withstanding freezing, which is not the case with other evaporimeters. However, it has one disadvantage. It is a difficult matter to standardize it, and to compare its readings with those of other instruments.

(Methods of Recording Moisture Conditions.)

Methods of recording moisture conditions are, in general, methods of recording the measurements of the state of moisture or the change of phase of moisture.

(The most usual method of recording the state of moisture is by use of a recording hygrometer. This usually consists of a human-hair hygrometer with a lever which writes a record on a revolving drum.) These instruments are used in the U. S. Weather Bureau, and

are supplied by Julian Friez. They are, in general, fairly satisfactory, but must be standardized against a sling psychrometer. It is important in making the standardization to make sure that the instruments are equally well standardized at the two extremes of relative humidity. (There are also several forms of wet-and-dry bulb recording thermometers on the market. These are very satisfactory, but it is very necessary to see that the wick covering the wet bulb is always clean and properly moistened.) The principle of the recording resistance thermometer may also be used in connection with recording humidity by supplying one of two resistance thermometer bulbs with a wick.

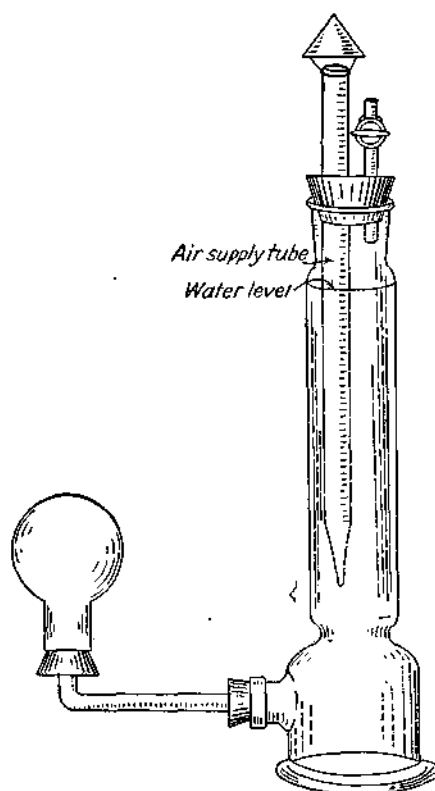


FIG. 34.—Reinhard's rainproof atmometer mounting.

and exposing them to the movement of air, as must be done in all psychrometric methods.

(Recording the change of state of moisture may also be done by various devices. It is possible to connect a float with the rain gage and write the record on a recording drum by means of a pen and lever, which must of course be protected from the rain.)

For recording evaporation, several ingenious devices have recently been described. Chalkley and Livingston (1929) have devised a method of recording the rate of evaporation through a float on mercury in a U tube, which represents the capillary pull of the atmometer against a

restricted water supply. Figure

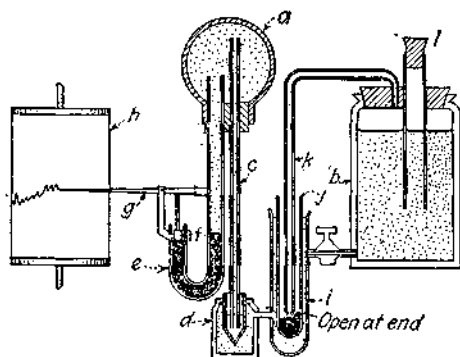


FIG. 35.—Diagram of the rate-recording atmometer: *a*, porous, porcelain sphere; *b*, main reservoir; *c*, water-supply tube; *d*, resistance member; *e*, mercury manometer; *f*, cork float; *g*, penlever; *h*, clock-driven drum for record sheet; *i*, auxiliary reservoir; *j*, float for water-level control; *k*, air supply tube to main reservoir; *l*, filling tube. (Chalkley and Livingston, 1929.)

35 shows this instrument. It has the difficulty of being complicated and requiring a number of tight joints. In the field work of the University of Minnesota, it has been found practical to use the special mounting of atmometer already described in Fig. 33 by making readings with a stop watch over 15-minute periods at various times during the day. These seem to represent very well the rates of evaporation under different conditions of the day.

Methods of Maintaining Constant Moisture Conditions.—The

control of humidity for experimental purposes involves humidification and dehumidification. Various simple devices may be used for humidifying the air. It is possible to maintain a small experimental chamber relatively constant by having a constant water surface exposed to the air where the temperature conditions are relatively constant. Dehumidifying, however, is much more difficult, and it is very necessary in experimental work. Experience has shown that, in general, it is better to employ standard apparatus for this important type of experimental work.

There are, in general, two methods of maintaining constant humidity. One is by the use of the dew point of the air, in which case the point of saturation of the air is controlled, and the ratio between this dew point and the ultimate temperature of the air controls the relative humidity. The second method is the use of solutions of various vapor tensions which are calculated to maintain air in equilibrium with them at the proper relative humidity.

The principle which is used in the Carrier air-conditioning cabinet is very satisfactory in experimental work. The air is circulated continually through the cabinet, and at each circulation passes into a dew-point chamber and then to a heating chamber, on its way to the experimental chamber. Figure 36 shows the Carrier cabinets in operation in the

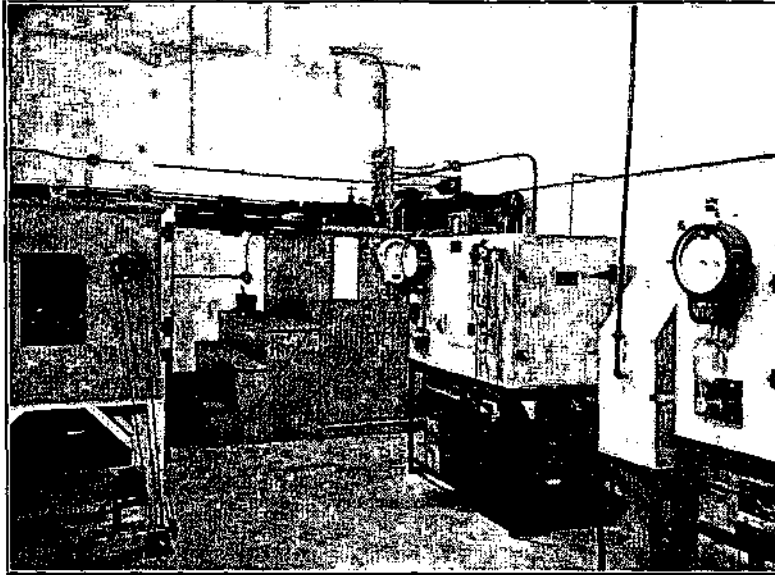


FIG. 36.—Carrier cabinets for the control of temperature and relative humidity in the temperature laboratory at the University of Minnesota.

temperature laboratory at the University of Minnesota. To the end of one of these cabinets is attached the dehumidifying chamber in which the air is cooled by coming in contact with water coils. The saturation of the air at the dew point is insured by an atomizer which blows a fine spray of water into the air when required. The humidity of the air is controlled through a silk-thread hygrometer. This hygrometer turns on the water in the atomizer when the relative humidity of the air is too low. Temperature is controlled by a metallic expansion thermostat. The dew point of the air will be limited by the ability of the machine to cool the air and to produce the spray at the temperature desired. It is possible to use a salt solution for the spray at dew points below freezing and to use refrigeration coils to produce low dew points.

Vapor tension humidifiers are satisfactory for certain experiments in small chambers. Sulphuric acid is also often used for this purpose. It is necessary to make sure that the air comes into equilibrium with the sulphuric acid. "International Critical Tables," Vol. I, may be consulted

for data on the solutions which can be used; also Wilson (1921) (Fig. 37). The air may be drawn through the solutions or forced through by pressure and should pass through a glass air-trap chamber before passing into the chamber where the experimental animals are kept. It is difficult to check the action of these solutions and to keep the sulphuric acid standardized as to specific gravity, as it obviously will gain or lose water depending upon whether it is humidifying or dehumidifying the air. It has been found practical to mount a small wet-and-dry bulb thermometer in a tube and to connect this with the air stream at times, in order to check the relative humidity.

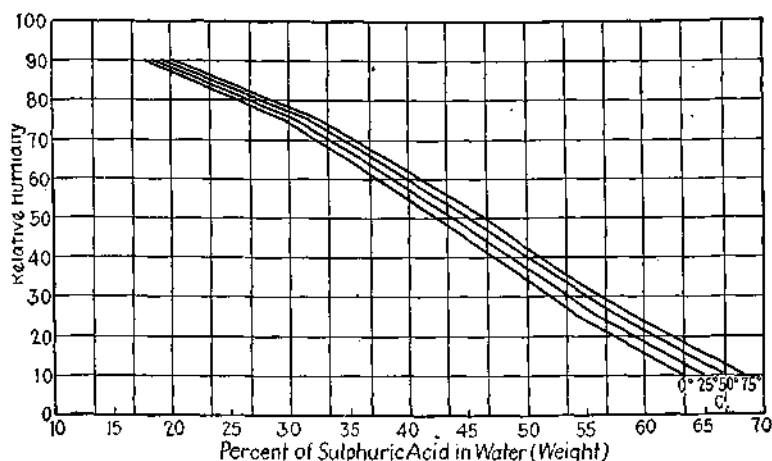


FIG. 37.—Graph showing the percentage by weight of chemically pure sulphuric acid in water required to produce various percentages of relative humidity when in equilibrium with air at different temperatures. (Data from Wilson, 1921.)

Headlee (1917) used supersaturated salt solutions in place of the sulphuric-acid solutions for obtaining certain constant-humidity conditions. The following table gives a list of convenient salt solutions which may be used in this way. It is necessary to use chemically pure salts and to make sure that the air comes into equilibrium with the saturated solution. This method has the advantage in that, if there is some precipitated salt in the bottom of the container and some water on top, it is supersaturated and, therefore, a standard solution is being maintained. It has been found that these solutions work better in humidifying than in dehumidifying. Consequently, it has been the practice to pass the air first through chemically pure sulphuric acid of a specific gravity of 1.84 and then through the salt solution desired. Difficulty is always experienced because of the fact that salt precipitates on the tubes where the air passes through the solution. These need to be cleaned almost daily. Difficulty has also always been experienced in obtaining the theoretical values for relative humidity. It is always necessary to

check the relative humidity which is being obtained by the use of the wet-and-dry bulb thermometer in a tube. This wet-and-dry bulb thermometer must also be standardized against air of known relative humidity, which is being moved through the tube at the same rate as the air in the experimental chamber.

TABLE VII.—TABLE OF THEORETICAL VALUES OF RELATIVE HUMIDITY OBTAINED WHEN AIR IS IN EQUILIBRIUM WITH SUPER-SATURATED SOLUTIONS OF CERTAIN SALTS¹

Salts	Percentage of relative humidity at 27°C.
Lithium chloride (LiCl) ²	7.164
Calcium chloride (CaCl ₂).....	25.97
Sodium hydroxide (NaOH).....	30.72
Aluminum chloride (AlCl ₃).....	37.01
Copper nitrate [Cu(NO ₃) ₂].....	45.71
Sodium bromide (NaBr).....	56.18
Sodium chloride (NaCl).....	73.414
Sodium nitrate (NaNO ₃).....	80.035
Potassium sulphate (K ₂ SO ₄).....	89.78

¹ Headlee.

Shelford (1929) gives a good discussion of the maintenance of constant relative humidity conditions. In experiments where it is necessary to maintain the evaporating power of the air at a constant rate, this may be done by controlling the relative humidity, the temperature of the air, and the rate of flow. Evaporation may be measured by introducing an atmometer into the stream of air to read the rate of evaporation.

For maintaining the moisture content of soil at a constant, it is most practical to weigh the soil and add moisture at regular periods to make up for the loss of evaporation.

For all experimental work under controlled moisture conditions, it is necessary to study the problem to be investigated and decide on the basis of each problem what type of control will be best adapted to the problem at hand. ?

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(Animals participate in the general moisture cycle of nature, in that they are continually taking in a certain quantity of moisture and losing a certain quantity. They, therefore, may be affected by the moisture cycle of their own metabolism and by the general moisture cycle of the environment in which they live.) (The atmosphere involved in their respiratory exchanges, the medium involved in their nutrition, and the general cycle of precipitation and evaporation in their surrounding medium, all affect them.) It is oftentimes difficult to analyze the situation

and determine which of these various effects is the more direct and the more important.

Bachmetjew (1907) summarized the early literature on the effect of moisture on insects; and since that time there have been various papers, some of which are listed in the bibliography. We have, however, no comprehensive summary of our knowledge on this subject at the present time.

Effects of Moisture on Physical Processes.—As in the case of other physical factors, before proceeding to study the effects of moisture upon organisms, we shall now pause to examine the effects of moisture on physical processes. Since all organisms are essentially aqueous solutions, we shall study the effect of various concentrations of materials in aqueous solutions. If we change the density of a salt solution, we change the various properties of it. The Table VIII shows the effect of the change of density of various salt solutions upon the surface tension as expressed in dynes per square centimeter. Inasmuch as surface tension is a very important factor in the mechanism of tissues and cells, we can see that they may very well be affected by the moisture content in this physical way. If we were considering the rate of contraction of the cells or the rate of division of cells, it is easy to see that they would be greatly influenced by such changes in surface tension as are expressed in the table. Inasmuch as this is largely a physiological question, we shall not take more time to present further examples of the effect of moisture content upon the mechanism.

TABLE VIII.—THE RELATION OF THE DENSITY OF AQUEOUS SOLUTIONS TO SURFACE TENSION

Solution	Density	T.°C.	Surface tension dynes per cm.
NaCl in H ₂ O.....	1.107	20	80.5
NaCl in H ₂ O.....	1.193	20	85.8
CaCl in H ₂ O.....	1.277	19	90.2
CaCl in H ₂ O.....	1.351	19	95.0

Effects of Moisture on the Rates of Biological Processes—Growth, Metabolism, Etc.—The evidence of the effects of moisture upon the rates of metabolism in general is very incomplete. (We have, however, data for certain particular organisms which show that they have an optimum moisture condition and that above and below this there may be a depression.) This is in accordance with the information which we already have on other physical factors. In examining the lists of examples which we have from research, (it is evident that it is not always possible to measure the effect of humidity upon the rate of metabolism alone,

Mortality may sometimes be a better measure of the effect of humidity than rate of metabolism. (It is also found that different stages in the life cycle of a single species differ more in their humidity relationships than do the same stages of different species.)

(Dendy and Elkington (1920) found that the rice weevil, *Sitophilus oryza*, required about 10 per cent of moisture in wheat in order to develop. In this case the larvae are entirely surrounded by their medium, as they burrow into the center of the wheat berry, and are therefore affected very largely by the moisture content of their nutritive medium.)

(Newstead and Morris (1920) found that the mite, *Aleurobius farinae*, developed rapidly when 13 per cent of moisture was present in the flour, but that development was slow at 12.4 per cent of moisture, and that the mites died in about two weeks when the moisture was reduced to 12.2 per cent. This seems to indicate that certain forms at least are extremely sensitive to moisture content.)

(Elwyn (1917) found that 100 per cent of relative humidity was the optimum condition for the development of *Drosophila*, and that a lower humidity greatly increased the mortality. However, the rate of development was found to be the same for 100 per cent, for 60 to 66 per cent, and for 0 per cent so long as the food medium was maintained properly. Dewitz (1902) reported a similar condition for *Lucilia*.)

Parker (1915) studied the development of the sugar-beet root louse, and found that they might be killed by the addition of excess moisture to the soil. Moisture in this case has an important effect upon the hatching of eggs and the molting of the skin in the immature stages and the general development of the insects. In an experiment, Parker introduced a lot of 200 sugar-beet root lice under each of three conditions: (1) in dry soil; (2) in soil which was subirrigated; and (3) in soil which was wet from above through a method simulating a rain. When these conditions were maintained for two months, he found that in the dry soil the population had increased to 11,581. In the experiments which were subirrigated, the population had increased to only 750; and in that which had been wet, through frequent showers from above, to only 405. Two series of experiments gave essentially the same results.

(Headlee (1917) chose *Mylabris (Bruchus) obtectus*, the bean weevil, for his experiments. These larvae burrow into the bean and live entirely within the bean, using the moisture content of the bean and their own metabolic moisture to maintain themselves. The beans, in turn, tend to come into equilibrium with the surrounding air. For this reason, Headlee considered that this species was well adapted for experiments to determine the effect of relative humidity upon the rates of development.) The accompanying graph is taken from Headlee's data, and it shows that in general the development of larvae is most rapid at high relative humidity (Fig. 38). (In studying the pupal stage, however, it was found that the

development was more rapid at low humidities, being 22 days at 100 per cent and 14 days at 44.6 per cent. The eggs also hatched in six days at 100 per cent, and in four days at 23 per cent.) In the case of this insect, one can get an algebraic sum of all the various effects of the different stages, which gives a shortening of the total life cycle at higher relative humidity as compared with the lower relative humidity.

(In the study of other insects, Headlee (1917) found that the pupal period of the moth, *Sitotroga cerealella*, was lengthened by high humidity, being 17 days at 100 per cent and only 12 days at 21.8 per cent.)

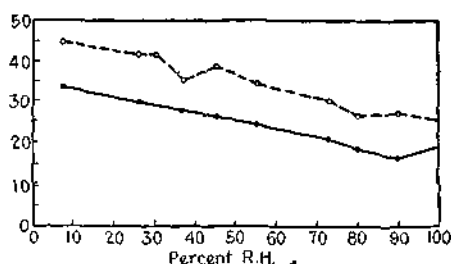


FIG. 38.—The development of the bean weevil (*Mylabris oblectus*) at constant temperature and various percentages of constant relative humidity. Broken line, one experiment; solid line, average of three experiments.

(In earlier studies, Headlee (1913) found that *Toxoptera*, the green bug which feeds upon various small grains, developed at the same rate at 80°F. when the relative humidity was maintained at 37, 50, 70, 80, and 100 per cent. This seems to indicate that certain organisms which feed upon the sap of plants may be relatively independent of the direct effect of the humidity of the surrounding

air. It is even possible that in some such organisms their problem is to dispose of excess water, rather than to be sure of maintaining a certain minimum of water.)

Hennings (1907) obtained results from a study of *Typographichus*, a beetle which lives under the bark of trees, and found that the comparison of moist and dry conditions showed that the development was retarded by moist conditions. His experiments were run at temperatures of 14, 17, 20, and 24°; and he found that where the experiment under moist conditions was compared with that under

dry, development was retarded 13 days at 14°, 7 days at 17°, 7 days at 20°, and 6 days at 24°C. It is possible that in this case there may have been a complication due to the development of fungi giving some biotic resistance.

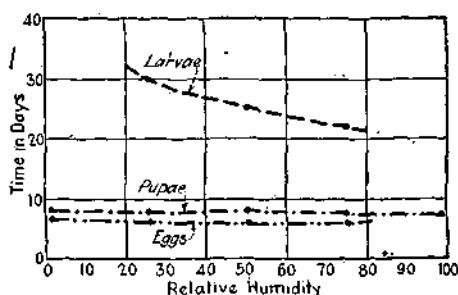


FIG. 39.—Duration of the stages of *Tribolium confusum* Duval at different relative humidities and 27°C. (Holdaway's Thesis, 1928.)

(Holdaway (1928, unpublished thesis) studied the development of *Tribolium confusum* at various relative humidities under constant temperature conditions. He found that the egg and pupal stages were of almost exactly the same duration throughout the entire scale of relative humidity. The length of larval life, however, was shortened by increasing the humidity, as shown in Fig. 39. From the standpoint of per cent of mortality, however, he found that there was a greater survival of the larvae at high humidity, but a reduced survival of eggs and pupae, as is shown in Fig. 40.) The larvae, therefore, have their per cent of survival increased and the length of time for development decreased by an increase of humidity; while the pupae and eggs do not have the time change but have the per cent greatly reduced by high humidity. It was true, however, that the greatest difficulty at high humidities was biotic resistance from fungi.)

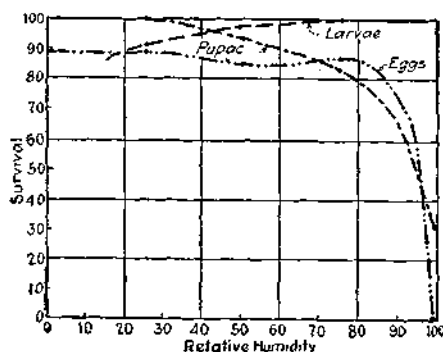


FIG. 40.—Viability of the stages at different relative humidities. Constant temperature of 27°C. (Holdaway's Thesis, 1928.)

(Davies (1928) studied the effect of various constant-humidity conditions upon a series of species of *Collembola*. He measured the length

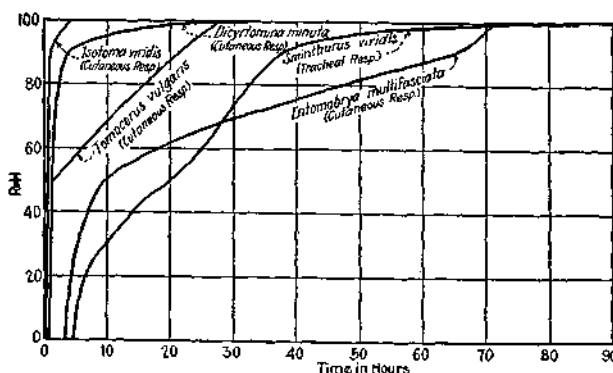


FIG. 41.—Fifty per cent mortality plotted against time and percentage of relative humidity. (Data adapted from Davies, 1928.)

of time which populations of *Collembola* could survive under starvation conditions, and took this time as a measure of the effect of humidity. It is quite possible, as he recognizes, that at some of the longer times the factor of starvation may have been important. The general results of his experiments are graphed in Fig. 40. This gives a series of species

with various susceptibilities to low relative humidity. It is interesting to note that *Sminthurus viridis* has tracheal respiration, while the rest of them have cutaneous respiration. It is Davies' view that, in general, organisms with tracheal respiration are less susceptible to low humidity than those with cutaneous respiration. He believes that in the case of *Entomobrya multifasciata* there is some physiological adjustment in connection with the surface respiration. It is quite possible that the systems of evaporation from insects with and without trachea are quite different. Where trachea are not present, we have the simple matter of diffusion over the surface of the body. Where trachea are present, there is diffusion through the tracheal walls into the lumen of the tracheoles and then the process of diffusion from the openings of the spiracles.

Hazelhoff (unpublished) has said that he found no effects upon the opening and closing of the stomata of cockroaches due to different relative humidities, which seems to indicate that this organism was not reacting to humidity in so far as controlling diffusion by the opening and closing of the spiracles was concerned.

(Heavy precipitation may act directly by mechanically removing certain insects from their host plants. This is common knowledge with regard to many plant lice, and it has been observed as an important factor in reducing the number of larvae of the larch sawfly, *Lygeonematus ericsonii*, by washing them to the ground where they are unable to regain a place on a host plant. Hail may also reduce the population of foliage-feeding insects as well as damage their host plant.)

Carter (1927) suggested that the concentration of sap in plants in desert regions may have an important effect on the insects which feed upon them. As the soil moisture becomes reduced, the concentration of cell saps not only increases, but the sap is less abundant. Consequently, in the semi-arid regions, as the summer advances, organisms are forced to leave the plant, partly because of a reduced amount of sap and, partly, because of the concentration of the sap that is present.

(Burger (1907) fed the meal worm, *Tenebrio molitor*, on dry bran, and found that the larvae lost weight but maintained their moisture content as almost constant until they died. After death the moisture was lost.)

(Babcock (1912) found that the larvae and adults of *Tribolium confusum* maintained a moisture content of around 50 or 60 per cent, while the moisture content of their food was in the neighborhood of 10 per cent. This seems to indicate that many of the insects are capable of maintaining the moisture content of their tissues as relatively constant.)

Robinson (1928) graphed the relationship between the total water of food and the total water content of insects, as shown in Fig. 42. The heavy line drawn across the graph indicates a perfect correlation between the water content of the food and the water content of the insect. All

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of those forms which have a higher water content in the body than the food are adding to the water content of the food the water of metabolism. Some of the species which live upon food of very low moisture content must depend very largely upon the water which they get as a by-product of their metabolism. It will be noticed that in most of the cases the water content of the insect bears some relation to that of the environment. The upper, or broken, line presents a hypothetical condition in which the moisture content of the insect would be exactly the same as that of the environment. None of the cases falls on this line, and only two or three occur in its vicinity. This indicates factors other than those which come into effect in the total water content of the insect. The degree of the deviation of the broken line indicates the extent of the influence of these other factors.

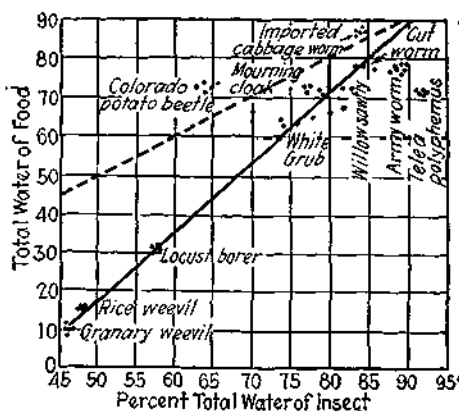


FIG. 42.—Relationship between water content of insects and their food. (Robinson, 1928.)

The water binding capacity of the different species is shown in Fig. 43, where a correlation has been made between the total water of the individual and the amount which is held in a bound condition on the

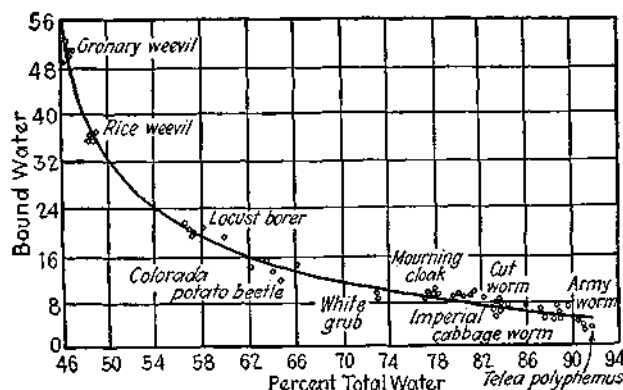


FIG. 43.—Relationship between water content and percentage of it which is bound by colloids. (Robinson, 1928.)

colloids. Those species which live on comparatively dry food and have a small percentage of water in their own tissues hold a large per cent of it in the bound form, which is secure against the forces of desiccation. For instance, the granary weevil, which has only 46 per cent total water,

has 50 per cent of this in the bound condition. The rice weevil, with slightly more total water, namely 48 per cent, has a smaller portion, or 35 per cent of it, as bound water. The locust borer, with 50 per cent total water, binds 20 per cent. At the other end of the chart are the species which live on food high in water and which consequently have a high content of water themselves. A reverse order of conditions exists here; with from 58 to 92 per cent of water in their tissues, they have only a small amount of this as bound, varying from 9 to as low as 3 per cent.

(These results seem to indicate that various species of insects have various physiological adjustments to protect themselves against the desiccating action of their environment. It is quite evident that it is necessary to know something of the physiology of the insect as well as the moisture relations of the environment in order to make a correct interpretation of the effect of the environment upon the insect.)

(If we were to generalize from the evidence before us, it seems safe to state that, in general, if insects have a moisture supply secured directly or indirectly through their food, which makes it possible for them to maintain the moisture content of the body, they are relatively independent of the moisture content of the surrounding medium. However, the moisture content of their food is affected by the surrounding medium. Consequently, there is always an indirect effect of the surrounding medium upon the insect. There may be also a direct effect in the event that the evaporation rate may be so great that they are unable to maintain a moisture content from their food source. Ecological literature, however, seems to be in need of a general summary on the effects of moisture upon insects, both physiologically and ecologically.)

Effects of Moisture on the Morphology of Animals.—Turning our attention to the effects of moisture upon the structure of insects, we might consider the types of structure which are normally correlated with moist environments, and those which are normally correlated with dry environments. In this consideration, it does not necessarily follow that the structures which are present in dry environments and which seem to be adapted for protection against evaporation are necessarily developed because of the dry environment. And the same may be said with regard to the structures which are found in organisms living in moist environments. In previous paragraphs, reference has been made to the correlation between rate of evaporation and type of respiration in insects. Surface respiration is correlated with a very thin cuticula, and the heavy chitinous covering is associated with tracheal respiration. In the case of an insect covered with heavy chitinous covering, evaporation must take place mainly between the tissues and the tracheoles; and diffusion, then, takes place through the spiracles from the tracheal system to the surrounding atmosphere. Insects which fly rapidly through the air and are therefore exposed to conditions which will produce a very high rate of

evaporation have well-developed tracheal systems and also tracheal air sacs. It is an interesting suggestion that these tracheal air sacs may act in conserving the moisture of the insect. The per cent of reduction of moisture content of the air in the large sac because of diffusion through a small opening is much less than that through an opening into a small lumen.

Literature seems to furnish us with very few cases of unquestioned evidence of the effect of humidity upon the structure of animals. The following table is given by Bachmetjew taken from data from Quajat.

Race of silkworms	Number of cocoons per "1 ko"		
	Dry air	Moist air	Normal
Round Chinese white.....	771	705	754
Yellow Indian.....	442	409	403
White Japanese.....	653	593	623

In all cases the silkworm seems to have produced larger cocoons when the larvae were reared in moist air. This seems to be fairly representative of the effects of humidity upon insects, but there is little in the way of definite data to support the generalization.

Andrews (1916) showed that the color of the rhinoceros beetle, *Dynastes tityrus*, is influenced by the moisture content of the atmosphere. Under moist conditions the chitin appears dark; under dry conditions, it appears light.

The effects of moisture on color seem to lack proof. Knight (1924) at first considered that moisture was an important factor in conjunction with temperature, in producing the color changes which he observed in *Perillus*. Later, when it became possible to control conditions with greater accuracy, he concluded that moisture was of minor importance. Thus, it is possible that much of the work summarized by Bachmetjew (1907) and scattered through the literature since that date, may be in error with regard to the effect of moisture.

Effects of Moisture on the Behavior of Animals.—Animals in many habitats have the opportunity to select the conditions of moisture in the same way that they may select light or temperature under other conditions. Literature of economic entomology cites certain cases in which moisture has been used in connection with insect traps (Dendy and Elkington, 1920).

Shelford (1914a and 1914b) and certain of his students and Hamilton (1917) studied the reaction of insects to air of different evaporating powers. An experimental gradient cage was so arranged that three

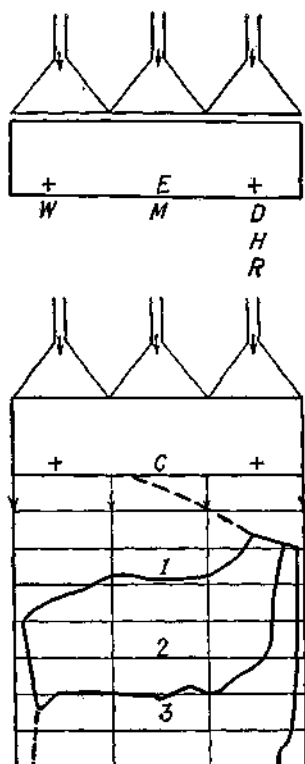


FIG. 44.—Showing the ground plan of the experimental cages in their relative positions. The hood which covered and separated them is not indicated. *E* is the experimental cage; *W*, the section used for wet air; *M*, for the air supplied directly from the pump; *D* (dry), *H* (warm), and *R* (rapid flow) indicate the section where the highest rate of evaporation was maintained. The crosses indicate the positions of the 1 candle-power lights; the arrows, the direction of the flow of air. The screen portions of the cage are represented by broken lines. *C* is the control cage similar to the experimental in every way except the kind of air supplied. Below this is shown the control record of an experiment during the first three minutes. The ruling of the paper used corresponds to half minutes and the figures are written in at the center. (Shelford, 1914.)

conditions of evaporating power of air could be moved across the cage (Fig. 44). The evaporating power of the air might be due to the rate of movement of the air, to the temperature of the air, or to the relative humidity of the air. The organisms were introduced in the center compartment of the cage and permitted to move back and forth. If they were sensitive to a difference in the evaporating rate of air, they would usually choose one side of the cage or the other. A record was kept on graduated paper in such a way that the path of the beetle back and forth across the cage could be shown by one dimension, and the time by the second dimension. (The diagram (Fig. 45) represents results which

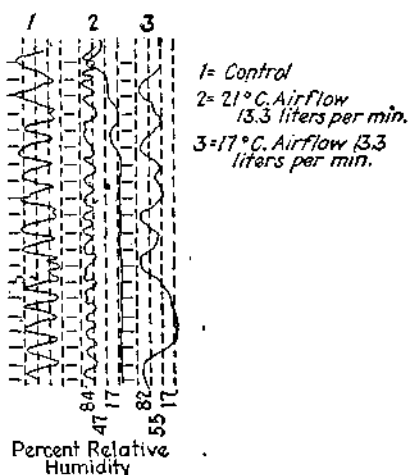


FIG. 45.—Reactions of *Evarthus sodalis* to moisture. (Hamilton, 1917.)

were obtained by Hamilton (1917) studying the reactions of larvae of one of the carabid beetles, *Evarthus sodalis*. The three vertical columns in each experiment represent the air in the gradient, and the passage of time is indicated on the vertical scale. Certain individuals reacted more definitely than others. In general, it seemed that those insects which are normally exposed to gradients of evaporating power of air have the most precise reaction. Others are relatively indifferent to it.

Robinson (1926b) experimented with the reaction of certain grain weevils. These were introduced into a glass tube in which there was present wheat of various moisture contents. The experiments could be run for only a short period of time because of the fact that the wheat in the various parts of the tube tended to come into equilibrium with wheat in other parts. In this case it was not a simple reaction to moisture content, but a feeding reaction which was involved. Some of the wheat was too dry for the weevils to feed upon. The amount of frass which accumulated in the various sections of the tube was an index of the amount of feeding which was done in these places.

Certain wood-boring beetles seem to be very much influenced by the moisture content of the wood in which they are able to work. Soil insects undoubtedly react to soil moisture content in a rather definite way. The flight of many nocturnal moths seems to be influenced by relative humidity; as darkness comes on, at the end of the day, temperature falls and relative humidity rises. Our present discussion of the subject cannot be taken as final, but as an introduction to a subject which needs further investigation.

Effects of Moisture on the Geographic Range of Animals.—Temperature and moisture are so interrelated in controlling the geographic range of organisms that the two are often confused, and it is difficult to separate out either moisture or temperature as a definite controlling factor in the geographic distribution of animals. The subject is to be treated later in connection with climatology and with the geographic distribution of animals.

CHAPTER V

EFFECTS OF TEMPERATURE AND MOISTURE ACTING TOGETHER IN THE ECOLOGY OF ANIMALS

In measuring the effects of temperature and moisture upon animals, it has always been necessary to maintain all other factors as equal and constant when the effect of one was being measured. This is true of the analytical work of all ecology; and it is also true that in the conditions of the environment in general, when one factor changes, other factors are involved in the change also. It seems wise to stop at this time to consider what effect there may be from several factors varying together. We have just considered temperature and moisture, two of the most important and most fluctuating of the factors of environment, and it seems well at this time to consider the action of the two together as an illustration of the action of two environmental factors.

In this consideration let us make the distinction between the effect upon the organism of the two factors varying together and the effect upon the environment when two factors vary together. For convenience we shall consider first the effect upon the organism. It is true not only that temperature and moisture are associated in their natural fluctuations in nature, but that the effect of one is modified by the changes in the other. The information which we have with regard to the combined action of these two factors has come to us as a result of the two general methods which we possess for obtaining information with regard to natural phenomena. One is by the use of controlled laboratory experiments in which all conditions are made constant except those which are to be changed for the purpose of observing what effects may be produced by the changes. This method has certain obvious limitations of space and time in the conditions of the experiment and of the perception of the human senses in observing the effects. The other method is to take the facts from the conditions which exist in nature, and experiment with them by the use of refined biometrical methods which are capable of detecting certain effects which are not noticeable by general observation. This method has limitations due to the lack of available facts, and both methods are subject to faults of reasoning.

When we express the effects of two factors, we can do it most conveniently on a two-dimension surface, as will be shown presently. If we were to use more than two factors, we would require a three-dimension surface. We might even visualize a theoretical sphere, each diameter

of which represents the dimension of some factor of the environment. The optimum condition of the organism would then be at the center of the sphere. We could make this figure a sphere by arbitrarily adjusting the length of each diameter so that the limits of toleration of the organism would always fall at the surface of the sphere. The outer surface of this sphere, then, would represent the limits of toleration of the organism with regard to all the factors of its environment; and the center of the sphere would represent the optimum condition with respect to all the factors of the environment.

Liebig recognized the fact that, when a multiplicity of factors was present and only one was near the limits of toleration, this one factor would be the controlling one. This generalization has been called "Liebig's law" and is useful in the analysis of complicated factorial influences.

Effects of Temperature and Moisture on Physical Processes.—Before proceeding with the effects of two factors upon a complicated organism, it will be well to look again to simple physical systems to determine what effects may be produced by changes of both moisture and temperature together. This is obviously a repetition of facts which are of common knowledge. Any constant on a physical scale is a constant only when all factors are involved as stated. The boiling and freezing points of all solutions may be changed by changing the concentration of the solvent in the solute. The freezing and boiling points of water are depressed when a material is put into the solution. One gram-molecular weight of dissolved substance in 100 c.c. water depresses the freezing point 18.7°C . The freezing point of ethyl dibromide is depressed 118° in this way, nitrobenzene 70° , and benzene 49° . In a similar way the boiling points of solutions may be elevated, and the elevation bears a constant ratio to the gram-molecular weight of dissolved substance. The boiling point of water is elevated 5.4°C . for one gram molecule of dissolved substance in 100 c.c. Since the water content of an aqueous solution varies the boiling and freezing points so much, it may be expected that the water content of a complicated organism will greatly affect the behavior of the organism in respect to temperature.

Effects of the Combined Factors of Heat and Moisture on Animals.—The facts with respect to the effects of temperature and moisture on physical systems, which we have just recited, will give a background for the understanding of physiology of cells, which are after all aqueous solutions. We now must turn our attention to an organism in which these cells are combined into tissues, and the tissues into the entire organs which constitute the organism. And the organism is presided over by certain governing processes and in general by physiology. Some of these governing processes have to do with the regulation of the temperature of the entire organism. Much attention has been turned to this,

but it will be well to consider some of the generalizations of Hill (1908, pages 268-270).

For organisms in general, a moist cold atmosphere causes the organism to cool rapidly because of the rapid conduction of heat from its body in the moist atmosphere. Poikilothermic organisms have their metabolism decreased rapidly under these conditions, while homoiothermic animals are stimulated to increased metabolism in order to maintain their body temperatures.

In a cold but dry atmosphere, the heat loss will be less rapid because of less rapid conduction; and consequently, poikilothermic animals will have their temperatures reduced less rapidly, and homoiothermic animals will receive a less marked stimulus to increase their metabolism.

In a dry, warm atmosphere, evaporation on the surface of the body will be rapid. Consequently, there will be a cooling effect due to the heat of evaporation which will be lost by the animal. This makes the regulation of body temperature possible under high temperature in both poikilothermic and homoiothermic animals, for they are both alike in their lack of ability to reduce their temperatures in any other way than by evaporation from the surface, except as they may slow their general metabolism.

A moist, warm atmosphere does not permit evaporation on the surface of the body; and with rapid conduction there is no method for lowering the temperature of the body, and the animal very shortly comes into equilibrium, with the temperature of its body similar to that of the surrounding air.

There is no implication that this interpretation of the interdependence of temperature and humidity is especially new. It has been known for a long time, and in many cases recognized, that the effect of humidity is so slight that the temperature scale might be used alone, almost ignoring humidity. Inasmuch as we are especially interested in the effects of temperature and moisture upon insects, we will turn our attention to the graph of Pierce (1916), in which the effects of temperature and humidity are shown on a two-dimension surface.

The data used by Pierce were those from field notes, and the zones that he has drawn are hypothetical to a certain extent. But he illustrates the possibilities of this method of treatment from data. In Fig. 46 the dotted lines across the chart represent the cross-sections through the optimum temperature and the optimum humidity respectively. It may be seen that the weevils will be dormant at the optimum temperature, provided the humidity is extreme, or may be dormant at the optimum humidity, providing the temperature is extreme. The various combinations of temperature and humidity which produce equal effects upon the boll weevil are shown. There is a small zone about the optimum-temperature humidity in which development is most rapid. In

any direction from this zone, development is slowed; and we get the next zone of equal development. These concentric zones of equal development may be thought of as contours, indicating the level of development. If this conception were represented by a pyramid instead of a flat surface, the height of the pyramid would represent the rate of development, the fastest rate coming where the complete development takes place in the shortest period of time, at the intersection of the optimum temperature and the optimum humidity.

A somewhat similar figure was made by Huntington (1915) to represent the death rate of populations under different conditions of temperature and humidity on the days of the deaths.

It is interesting to note that the general nature of the figure obtained by Huntington was quite suggestive of that obtained by Pierce. However, the use of Huntington's data is open to a certain objection, as has been pointed out by the medical profession, because of the fact that it is not known definitely that temperature and humidity were a factor in producing death.

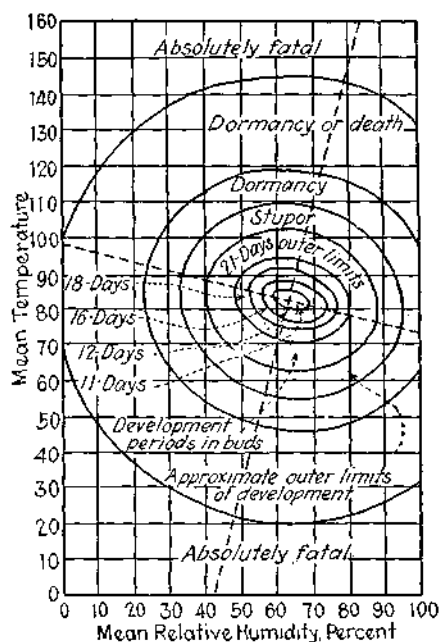


FIG. 46.—Graph showing the relations of humidity and temperature to cotton boll-weevil activity. (Adapted from Pierce, 1916.)

Another two-dimension surface to represent the effects of temperature and moisture has been plotted from the data of Parker (1930). In this case, however, the time for hatching was almost uninfluenced by relative humidity, and the surface presented is graphed for the per cent of hatching of the eggs. These eggs were maintained at different temperatures and humidities, as shown upon the graph in Fig. 47. The dots, and the figures by them, represent the per cent of hatch at the different conditions. The zones which are outlined in dotted lines have been interpolated. It will be seen that we have here an optimum relative humidity of about 90 per cent, and an optimum temperature of 27°. The per cent of hatching at 27° varies from 6 to 72, depending upon the relative humidity; and likewise the per cent of hatching at 90 per cent of relative humidity varies from 48 to 72, depending upon the temperature.

We can well be cautious in drawing broad generalizations from the examples which have been presented. The general nature of the effect

of the two factors acting together seems to be well established for either one of the factors as a two-dimension surface rather than as a straight line.

Shelford (1926 and 1929) had attempted to evaluate the factors of temperature and humidity in phenological units. He has plotted the cross-sections of such figures which represent the lines of equal effect of temperature and humidity. This is a promising field of future investigation; but it is also a field which must be gone into with caution, if we are

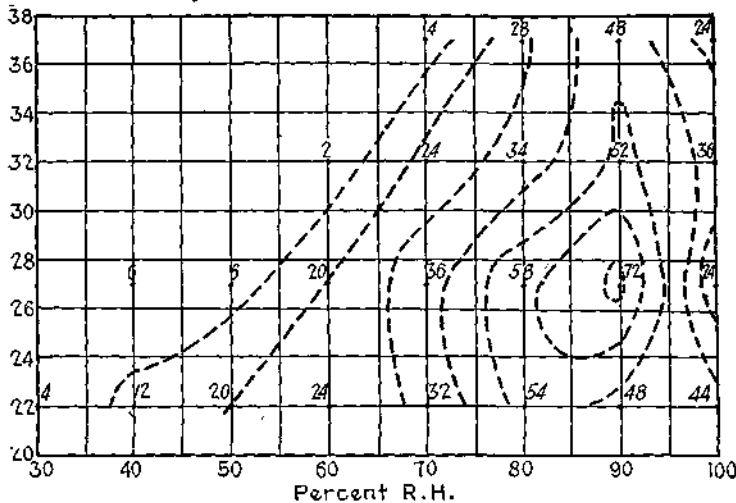


FIG. 47.—Graph showing the relationship between temperature and humidity and the hatching of grasshopper eggs. (Adapted from Parker, 1930.)

to draw generalizations which may be applied to species. The figures represented by the data of Parker and Pierce are alike, in that they show optimum zones and marginal zones in which, in the one case, mortality is extremely high, amounting to 100 per cent; and, in the other case, development is stopped, ending in dormancy, and beyond this going to death. But the optimum in one figure represents a high per cent of hatch, and the optimum in the other figure represents the highest rate of development. If we were to evaluate these in terms of a common denominator, that common denominator would have to be the change of population. This would also be true of many examples of insects which have been cited under the heading of the effects of heat and moisture; for their life cycle may be the same length under a whole series of humidities, provided temperature is constant.

However, death rates, and thereby population, may be affected by humidity. These concentric zones of temperature and humidity have been determined for relatively few organisms at the present time. Doubtless, future research will show that additional factors may be

added to extend these zones in another dimension. But it seems rather evident from the literature which we have available at the present time that our understanding of them is not sufficiently clear to warrant generalizations which may be applied to all.

The effect of moisture and temperature acting together on human comfort has been investigated by the American Society of Heating and Ventilating Engineers in rather an elaborate series of experiments.

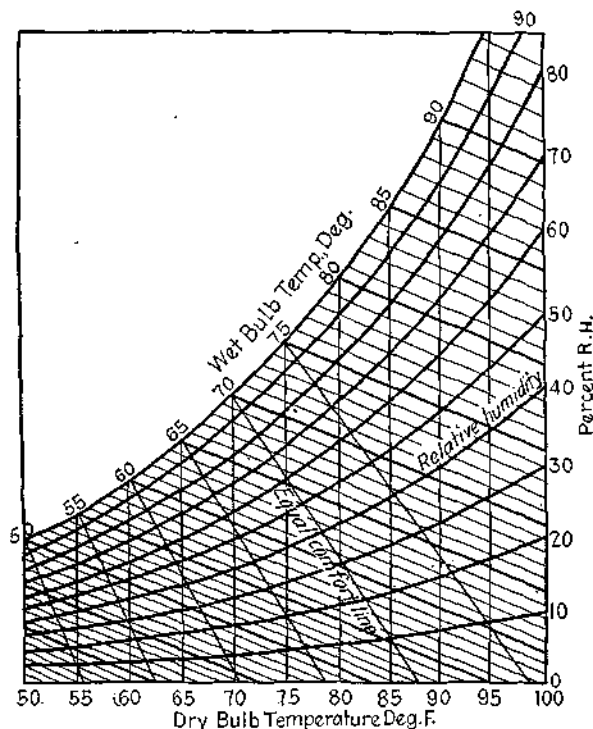


FIG. 48.—Chart of equal comfort or effective temperature. (All reference to temperature in degrees Fahrenheit.) (Houghton and Yagloglou, 1923.)

They have recorded the effects on internal and external body temperatures, pulse rate, blood pressure, rate of respiration, loss of weight, and various other measurable conditions under variations of temperature and humidity. A large number of subjects were permitted to enter chambers with different temperature and humidity conditions, and to record their sensations of comfort as agreeable, cool, warm, etc. When all of the data were assembled, they were found to be consistent in denoting that there are certain conditions of equal comfort. A chart was constructed (Houghton and Yagloglou, 1923) from which it is possible to determine the combinations of temperature and humidity which will give equal comfort. The two authors have referred to these

conditions as a scale of "effective temperature." This term is quite different from that which has been used previously, and is intended to denote a scale of equal effects rather than the usual thermometer scale. From the chart of equal comfort (Fig. 48), it is shown that an equal condition of comfort may be found at 68°F. and 80 per cent of relative humidity, or 79° and 10 per cent of relative humidity. Within these limits, the subjects considered that the temperature was at the optimum of comfort. Consequently, our dry-bulb temperature scale is shown to be unreliable as measuring our sense of the temperature.

Turning our attention briefly to the effects of moisture and temperature upon the environment, McDougall (1925) has presented an interest-

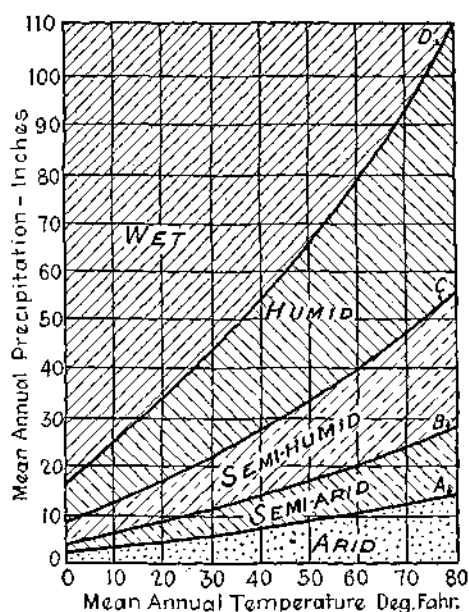


FIG. 49.—Chart of moisture, based on precipitation as influenced by temperature. (McDougall, 1925.)

ing conception which he has taken from Köppen (1920). It is, of course, well known that the significance of a certain annual precipitation depends largely upon the temperatures which accompany it, and thereby upon the evaporation. When precipitation and evaporation are equally balanced, there will be no excess of water to run off. In the diagram (Fig. 49) McDougall has taken Köppen's conception of this critical point where evaporation and precipitation are equal, and has drawn the line *B*, which represents the evaporation rates and precipitation rates which are equally balanced. Environments in which the conditions lie above this line are

classified as humid; and those which lie below it, as arid. All environments with less than half of the critical amount of precipitation are classified as arid; the others, as semi-arid. The consideration of environments will be referred to later under the subject matter of Synecology.

The ability of organisms to endure the extreme conditions of their environment is affected by both temperature and moisture, as may easily be seen by consulting the diagrams based upon the data of Parker and of Pierce. This is now generally recognized, as literature contains many examples substantiating this generalization.

Bachmetjew (1907) quoted data from various authors to show that albumen with 25 per cent water coagulated at 47 to 80°C.; with 18 per cent water, at 80 to 90°C.; with 6 per cent water, at 145°C.; and water-free albumen, at from 160 to 170°C. This indicates again that the mechanism of an organism is profoundly influenced by its water content, and that the temperature scale of an animal is affected by this.

With respect to the ability of organisms to endure extremely low temperatures, we have some critical information which has recently been accumulated. Payne (1926) showed that if the larvae of *Synchroa*, which normally burrow under the bark of trees and are exposed to low

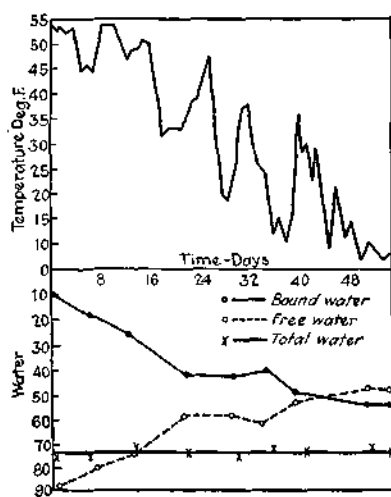


FIG. 50.—Effect of fluctuating outdoor temperatures upon percentage of bound and free water for the hardy *Telea polyphemus*. (Robinson, 1927.)

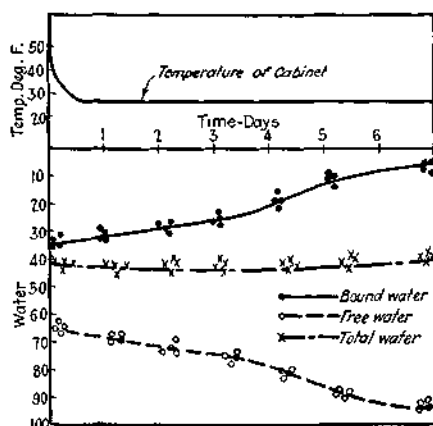


FIG. 51.—Showing reverse effect of a moderately low temperature upon the bound- and free-water content of the non-hardy *Sitophilus granarius*. (Robinson, 1927.)

temperatures in the winter, are dehydrated under laboratory conditions, their freezing points will be lowered.

Robinson (1927) compared the effect of moisture conditions at low temperature upon insects which were hardy at low temperatures with those which were not. He found, in general, that there was a change not only in the moisture content, but in the state of the water present in the insect. In *Telea polyphemus*, a hardy moth which hibernates in the pupal stage, the moisture content changes very little during the fall, as is shown in Fig. 50; but the per cent of water in the free state, and of that bound upon the surface of the colloids undergoes a marked change when the outdoor temperature drops. The pupae of this insect are capable of withstanding freezing for months. Figure 51 shows the moisture condition of *Sitophilus granarius*, a

weevil supposedly from the tropics, when temperature is being lowered. In this case there is a slight drop in total water, a decided drop in bound water, and an increase in free water; and the insects are unable to endure low temperatures. It seems, therefore, that the effects of extreme temperatures cannot be studied without being associated with moisture conditions, and that possibly death under extremes of the temperature is largely influenced by the moisture content and the state of the moisture in insects.

Payne 1929 has emphasized the importance of absolute humidity as expressed in millimeters of vapor pressure as an important factor in determining the intensity factor of cold which insects can endure. It seems quite definite from the work of Payne, Bodine, Fink, Robinson, and others that the ability of insects to withstand low temperature is usually limited by moisture conditions. In the case of insects which are able to withstand freezing of their free water, it seems that the proportion of water which they have bound on the surface of colloids may be a very important factor. The further changes which take place when temperature is extremely low are not well understood; but these changes seem to be irreversible and therefore fatal. The field of investigation of the effects of extremely low temperature is a very interesting and fertile one.

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APPENDIX TO CHAPTER V

DORMANCY

Dormancy will be used in this connection to cover all cases in which the development of an organism apparently ceases. It will, therefore, include the case of hibernation, or winter sleep; the case of aestivation, or summer sleep; the case of inanition, in which organisms are tiding themselves over a period of lack of food; and certain other cases in which it is impossible, at the present time, to assign a definite cause. Literature abounds in references to this interesting type of lethargy.

Polimonti (1912) summed up the theories of lethargy in an interesting volume entitled "Il Letargo." In 1916, Rasmussen gave a summary of the theories of hibernation. From time to time, almost every possible exciting cause has been taken up and sponsored as the one cause of dormancy. From a theoretical consideration, one may look over a diagram such as Pierce's graph of the effects of temperature and humidity, and see that either temperature or humidity or a combination of the two theoretically might produce dormancy. Similarly we might include all physical factors which may be beyond the limits within which organisms are normally active. It is for this reason that this discussion is entered into at the present time.

Before proceeding further with the discussion, attention will also be called to the fact that almost any physical reaction of an organism may be shown to be due in part to environment, and in part to hereditary constitution. The color of certain insects and, to a certain extent, their form and size may be varied by varying environment. Also, there may be genes which tend to produce certain form, color, and size almost regardless of the environment. The conclusion was reached in this discussion by Weinstein that the characters of an organism, like the area of a rectangle, are due not solely to one dimension. Just as the area of a rectangle varies both with the altitude and the base, so the characters of organisms vary both with environment and heredity. If we will now admit metabolism as a characteristic of an organism and consider, as has been very well demonstrated, that some organisms may have their metabolism proceed almost uninterruptedly and that others may require cessation of metabolism at certain intervals, we have another character, metabolism, which may be affected by both heredity and environment. We have many clearly demonstrated cases of cyclic metabolism, as in the case of reproduction in the oestrous cycle, the length of which has been

shown to be an innate hereditary character of given organisms, but which may be influenced to a certain extent by environmental influences. We turn our attention to the vast amount of literature which is before us on this subject, with this viewpoint in mind, granting that there may be cases in which heredity apparently plays the dominant rôle in that the characteristics of metabolism are definitely set down by it and are relatively unaffected by the environment. On the other hand, we will have cases in which environment plays the dominant rôle in determining the length of the period of activities and the length of the period of dormancy. It would seem difficult to draw a hard and fast line between cases of dormancy in which the environmental factors have relatively little influence and those in which they have a great influence, just as it would be difficult to draw the distinction between the effect of temperature in affecting the color of organisms and the influence of heredity in affecting their color; for in many cases the color of an individual may be due to both influences.

If the literature on the subject of dormancy is to be divided into groups on the basis of the types of organisms worked upon, we will find in one group the hibernating homoiothermic organisms which in the winter season might be said to cease to be homoiothermic and become poikilothermic. This is true of certain of the mammals; and Rasmussen (1916) gives a very good review of the various theories that have been proposed to account for this peculiar upset of the temperature regulatory system, and the adoption of a poikilothermic state. The most common theory of the cause of hibernation of these organisms is low temperature, but there are plenty of cases cited in the literature where the animals have not gone into hibernation under experimental conditions when exposed to low temperature. It has been suggested that the carbon-dioxide content of their burrows induces autonarcosis, but the work of Rasmussen on the woodchuck seems to have shown that this is not the case. Abundance of food and lack of food have both been proposed as a cause, and it has also been suggested that it is simply a form of sleep which is very profound. The work of Rasmussen on the woodchuck or marmot, and of Johnson on the striped spermophile are both good examples of the conditions which attend this dormancy in mammals.

Among the poikilothermic animals, the suggestion of the influence of low temperature seems to have carried much more weight, because here it is not necessary to postulate the upset of the mechanism for the control of temperature of the body. Among the insects it is perfectly clear that certain of these species can continue development generation after generation without any imposed dormant period. *Tribolium confusum* is such an insect. On the other hand, we have insects which pass through but one generation per year regardless of the fact that temperature is high enough for development to continue. In the north temperate

regions there are many examples of such insects. It happens also that there are certain species which pass through but one generation per year in the northern part of their range, and pass through several generations per year in the southern part of their range. These species have been the subject of a great deal of controversy. It seems evident in the case of many of these that if they were to start a second generation, the winter would catch them at a stage in which they could not endure low temperature, and the species would be wiped out. So we have the very interesting case of species which have either one or two generations per year, many of them without any attempt at an intermediate condition.

Roubaud (1922) proposed the term "holodynamic" for forms which continue their development without interruption, and "heterodynamic" for those which had their development interrupted by periods of dormancy. It seems, however, that the older terms, which have been in use in literature for a long time, of "univoltine" for those which pass through but one generation before dormancy, of "bivoltine" for those which pass through two generations in succession before dormancy, and of "multivoltine" for those with many generations, are more applicable. There is probably no single form which has received more attention from this standpoint than the silkworm, *Bombyx mori*.

Jueci (1924 and 1926) gives a very good statement of the problem in connection with the silkworm, which seems to indicate quite clearly that we have here a combination of environmental and genetic influences. This whole work has to do with the making of a distinction between cases in which environmental temperature is responsible for the oncoming of dormancy, and the cases in which no environmental influence is at least evident in causing the dormancy.

Roubaud (1922) suggested that in the cases where there is no evident environmental factor initiating dormancy, it may be due to an accumulation of waste product, such as urates. However, his theory requires that one conceive of the accumulation of these urates passing over from one generation to another. If they did so pass over, they would have to pass through the egg. It is difficult to conceive, quantitatively, of such an accumulation passing through the egg from one generation to another until the accumulation had reached such proportions that dormancy was induced.

Hormones and enzymes have been suggested as causing the dormancy. Such suggestions are not at all out of harmony with the theory that in many cases dormancy is a genetic factor, for we know perfectly well that in species where the period of the oestrous cycle is a genetic character it is in fact initiated by a hormone, the secretion of which is associated with the genetic factor. In the case of the European corn borer, *Pyrausta nubilalis* Hb., there are sections of the country in which there is but one generation a year, other sections where there are two generations a year,

and still other sections where there are sometimes one generation and sometimes two generations in a year. Babcock, Barber, Parker, and others have discussed the dormant period of the corn borer. It seems that the only attitude to be taken towards this problem is that many strains of the corn borer are heterozygous for univoltine or bivoltine factors.

Dawson (unpublished thesis) made a study of the polyphemus moth, which has but one generation a year in Minnesota, and two generations a year in Nebraska and points farther south. In this case, certain morphological differences are to be found between the two races, such as size and color of eggs, and other characters. He found, however, that under experimental conditions it was possible to induce the northern univoltine race to pass through many generations in one season, and also to get the southern race to pass through but one generation. However, in all cases there was a certain per cent of the population which did not behave as indicated. Extensive experiments, in which there was an attempt to select pure-line strains of bivoltine stock, indicate quite definitely that there are hereditary and environmental forces operating in this case, just as in nature the races are, to a certain extent, always heterozygous for the character of univoltine or bivoltine metabolism.

Looking at the problem from the standpoint of the general ecology of the organism, it seems evident that the environment is imposing upon the organism a period of dormancy by its selective action in wiping out all organisms which are not capable of enduring dormancy during the cold period of the year. The obvious result of this is the survival of the forms which have some method of passing this cold hibernation period. The question of how these organisms acquire the ability to hibernate is as mute as the question of the acquirement of any character.

Baumberger (1917) concluded that those organisms which could endure dormancy in whatever place the cold weather overtook them did not have a periodic hibernation period, but were controlled very definitely by the temperatures which obtained surrounding them; that those organisms which had to prepare themselves for hibernation by forming a cocoon or digging into the ground or otherwise protecting themselves, were characterized by a periodic dormancy, and that they began to prepare for it at a certain time, quite regardless of the temperatures that obtained at that time. With our present knowledge of the changes of physical factors, it is very difficult to distinguish between cases in which there is a definite periodicity and those in which there is an influence of the environment. At about midsummer, temperature begins its very gradual decline, the angle of incidence of the sun's rays changes, the food plant begins to mature, and a whole series of physical changes is under way though not very evident. A careful analysis of this entire situation with a complete citation of literature would require a volume in itself.

It has been the purpose to insert this little appendix on the subject of dormancy to suggest a viewpoint for the consideration of the whole case of dormancy.

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CHAPTER VI

PHYSICAL CONDITIONS OF ENVIRONMENTAL MEDIA

PRESSURE OF THE ENVIRONMENTAL MEDIA

The force which we measure as pressure of the environmental medium is that of the action of gravity on the superimposed atmosphere or water, although it may very well include the pressure which may be encountered in soil or in any other medium. Atmospheric pressure varies slightly in any given place with the changes in the general atmospheric conditions, but the greatest changes are those associated with altitude. *The possibilities for the change of atmospheric pressure which a terrestrial organism may encounter even when going to the highest altitudes are as nothing compared with the pressure which an aquatic organism may experience in going down even to the deepest parts of our lakes, to say nothing of the sea.*

Measurements in Recording of Pressure.—Pressure is commonly measured by means of a mercurial barometer which consists essentially of a tube in which the mercury in the vacuum column fluctuates with the atmosphere. The height of the column of mercury is a measure of the atmospheric pressure, when the temperature coefficient has been taken care of. If the instrument is exposed to a complete vacuum, there will be no column of mercury in the tube. If exposed to an ordinary atmosphere at sea-level, the column of mercury will be 760 mm. or practically .30 inches, and is equal to a pressure of 14.696 lb. per square inch, or 1033.3 g. per square centimeter. This is ordinarily stated as one atmosphere of pressure. The aneroid barometer registers the atmospheric pressure on a partially exhausted chamber. It is calibrated to read in the equivalent of inches or centimeters of mercury. These instruments are usually limited to a range of but a few inches, but are portable and require practically no correction for temperature. The more delicate aneroid barometers are often calibrated to read in altitude as well as in inches of mercury. They, therefore, make a very convenient instrument for making rough measurements of altitude when doing field work. The difference in altitude of two points may be calculated when the barometric pressures and the temperatures are known. There are more or less elaborate formulae which are very accurate, but the following approximate formula is practical where the differences of altitude do not amount to more than 1,000 m.

$$H = 1,600,000 \frac{b_1 - b_2}{b_1 + b_2} (1 + 0.004t)$$

In this case b_1 and b_2 are the two barometric readings, and t is the mean of the temperature of the two stations. It is often more convenient to determine the altitude directly from the scale of an aneroid barometer so calibrated, or from tables such as may be found in the "Smithsonian Meteorological Tables." Barographs for the recording of pressure usually operate on the principle of the aneroid barometer, which is connected with a lever and pen for writing on a revolving drum. Pressure at various depths and aquatic environments is usually calculated on the basis of the weight of the superimposed column of water, which amounts to one atmosphere for each 10.329 m.

The maintenance of various pressures or vacuums for experimental purposes may be maintained by the use of chambers and pumps. Pumps have now been developed which are capable of producing high pressures or a vacuum down to 0.001 mm. pressure. Some difficulty is experienced, however, in introducing pressure into laboratory experiments and adding it to all the other conditions which it is desirable to maintain at a constant. It is, however, by no means impossible with modern apparatus. The desirability of introducing it in any given experiment must be determined on the basis of the organisms involved and the type of experiment which is to be performed.

PRESSURE AS A FACTOR IN ANIMAL ECOLOGY

Effects of Pressure on Physical Phenomena.—All tables of the constants of physical phenomena designate the temperature under which the determinations were made. There are some physical phenomena which are profoundly affected by even a relatively slight change in barometric pressure. We all know that water boils at 100°C. at a pressure of 760 mm.; but at 775.2 mm. it boils at 100.6°C. At 660.2 mm. it boils at 96.1°C.; and at 431.8 mm. it boils at 84.9°. Therefore at an altitude of 15,430 feet, water will boil at only 84.9°C. It is very evident that evaporation will be greatly affected by such changes of barometric pressure as may be experienced in terrestrial environments.

Effects of Pressure upon Animals.—Knowing the effects of pressure upon the boiling point of water, we are not surprised that animals should be affected by changes in pressure. This is a case, however, in which it is extremely difficult to differentiate between the effects of pressure as such acting directly upon the organism and the effects of pressure upon other factors. It is difficult, if not impossible, to experiment with pressure and leave all other factors unaltered. When we experimentally reduce the pressure, we also reduce the pressure of the gases which are involved in respiration. Most investigations seem to show that metabolism in general is affected by the action of pressure upon the gases involved in respiration.

Herrera and Lope (1899) summarized the results of some experiments on the altitudes at which various organisms were found and were able to survive under equivalent pressures.

Schneider (1921) reviewed the literature on pressure, particularly of mammals, and gives data on the ability of various organisms, and especially man, to survive at different altitudes. It is shown that man becomes unconscious at from 23,000 to 25,000 feet; and this is due primarily to the changes in tension of carbon dioxide and oxygen. Carbon dioxide going from 39.7 mm. at sea-level to 30 mm. at 20,000 feet, and oxygen from 103.2 mm. to 34.8 mm. This allows for a difference in oxygen tension between the blood of capillaries and the alveolar air of only 5 mm., which means that it is no longer possible for the organism to take up sufficient oxygen and give off sufficient carbon dioxide to maintain normal metabolism.

Portier (1928) has arrived at the conclusion that birds are able to endure very much greater altitudes than mammals without suffering any difficulty. He has done this apparently entirely on theoretical grounds. He states that the respiratory mechanism of birds is so arranged that the inhaled air comes directly in contact with the blood capillaries and that the carbon dioxide is swept on ahead of it and is exhaled without mingling with the atmospheric air. In this way he considers that the carbon dioxide and oxygen tensions are balanced between the blood capillaries and the incoming air, whereas in mammals the incoming air mingles with and dilutes the carbon dioxide already present in the lungs. Thus he states that the difference in tension is much greater in birds than in mammals, and for this reason he believes that they are able to fly rapidly without difficulty at high altitudes. This reasoning might be applied to insects, as will be stated later under the consideration of gases.

Greenwood (1906) states that lesions are produced in animals, when they are decompressed, by the escape of nitrogen bubbles in the blood. He states that this would seem to be impossible in the case of insects, for he assumes that the blood performs no respiratory function. He experimented with larvae of *Cossus cossus*, and submitted two larvae to atmospheric pressures which he states as +25 and -30 for 20 minutes in the first case, and for 2 hours 40 minutes in the second case. These larvae pupated normally after being decompressed instantaneously. He concludes that this ability to endure the great change of pressure is due to tracheal respiration.

The literature on the effect of atmospheric pressure upon insects consists of that which is a result of experimental research with controlled pressures and from observations in the field under known barometric pressures. All experimental work seems to indicate that so far as pressure itself is concerned, insects are able to endure a reduction of pressure

EFFECT OF VACUUM VARYING FROM 24 TO 28 INCHES UPON INSECTS IN A CONCRETE VAULT CONTAINING 512 CUBIC FEET
 (Back and Cotton, 1925)

Insect	Killed in 3 days, per cent			Killed in 4 days, per cent			Killed in 5 days, per cent			Killed in 6 days, per cent			Killed in 7 days, per cent		
	Eggs	Larvae	Pupae	Eggs	Larvae	Pupae	Eggs	Larvae	Pupae	Eggs	Larvae	Pupae	Eggs	Larvae	Pupae
<i>Alphitobius piceus</i> Oliv.	...	90	90	100	100	100	...
<i>Anthrenus fasciatus</i> Hbst.	...	92	100	...	100	100	...	100	100	...	100	100	...	100	100
<i>Attagenus piceus</i> Oliv.	...	66	100	...	78	100	...	78	100	...	80	100	...	95	100
<i>Cryptolestes pusillus</i> Schon.	...	100	100	100	100	100	...
<i>Dermestes vulpinus</i> Fab.	...	100	100	100	100	100	...
<i>Ephestia kuehniella</i> Zell.	...	100	100	...	100	100	...	100	100	...	100	100	...	100	100
<i>Gnathocerus cornutus</i> Fab.	...	90	100	100	100	100	...	100	100
<i>Gnathocerus marillus</i> Fab.	...	90	100	100	100	100	...	100	100
<i>Necrobia rufipes</i> De Geer	100	100	100
<i>Oryzaephilus surinamensis</i> L.	50	65	90	100
<i>Plodia interpunctella</i> Hbn.	100	100	100	100
<i>Silvanus gemellatus</i> Dun.	100	100	100	100
<i>Sitophilus oryza</i> L.	100	100	100	100
<i>Sitophilus granarius</i> L.	100	100	100	100
<i>Tenebrio obscurus</i> Fab.	...	60	60	100	80	100	100
<i>Tinola bisellata</i> Hum.	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100
<i>Tinea pellionella</i> L.	...	100	100	100	100	...
<i>Tribolium confusum</i> Dun.	99	100	100
<i>Tribolium ferrugineum</i> Fab.	100	100	100
<i>Trogodema tarsale</i> Melsh.	...	20	20	30	30	...

which is more than equivalent to the highest altitude that may be experienced on the earth.

Cole (1906) exposed 10 rice weevils, *Sitophilus* (*Calendra oryzae*), which were placed in a vacuum of one inch of mercury with some food. On the fourth day three were dead; the seventh day, one; the twelfth

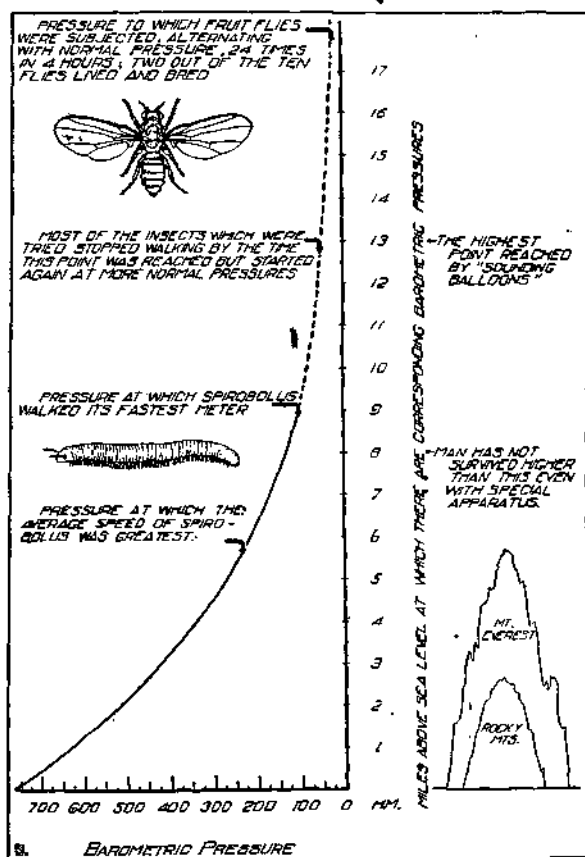


FIG. 52.—Summarizing certain experiments with reduced air pressure. The curved line shows approximately the relation between air pressure (horizontal scale) and height above sea-level (vertical scale) under normal conditions. At the right are human affairs, including diagrammatic representations of the heights of mountains. Entomological facts are given at the left. (Lutz, 1929.)

day, one; and the fifteenth day, five were still alive after they were taken from the chamber.

Back, Cotton, and others have shown that insects are capable of withstanding an almost complete vacuum for hours and even days, and that probably evaporation and respiration are responsible for death at the end of this time rather than the reduced pressure as such. The following table from the experiments of Back and Cotton shows how resistant

these organisms are. Lutz (1929) experimented with the milliped *Spiroboleus* and the fruit-fly, *Drosophila*. Upon measuring the rate of movement of *Spiroboleus*, he found it to be most rapid when pressure had dropped as far as nearly 100 mm. In the course of the experiments, flies, beetles, butterflies, and bees were exposed to supervacuum, some being able to survive at 1/10000 mm. for 90 seconds. The general results of the experiments are shown very graphically in Fig. 52. This seems to indicate quite clearly that insects are able to survive at pressures equivalent to altitudes greater than normally might be experienced on the earth.

We turn our attention to aquatic insects, such as *Corethra*, *Chironomus*, and others which live in the bottoms of our deepest lakes. We find that they are able to endure many atmospheres of pressure and even to emerge from the surface of the water after a rather rapid ascent without any bad effects. Further consideration of the pressures endured in the water will be taken up under the subject of Synecology.

The results of casual observation from the field usually state that flies are affected by a falling barometer. Parman (1920) reports that several species of flies go into a state of nervousness when the barometer is falling. He cites the example of *Stomoxys calcitrans* and the housefly, *Musca domestica*, which were particularly abundant just before the storm in 1916, but which could not be found in any numbers at all after the storm. There is of course no definite evidence that it was the falling barometer alone that affected these flies. Adult insects are said to emerge during times of high barometric pressure; butterflies also are said to migrate during times of high pressure.

Dodds and Hisaw (1925) concluded that the altitudinal distribution of lotic Trichoptera was due primarily to temperature, and that pressure associated with the altitude probably was an insignificant factor if of any importance at all.

We have little direct evidence with regard to the effect of pressure upon the development of insects. Lutz states that some of the *Drosophila* which were exposed to the lowest barometric pressures reproduced and their progeny were apparently normal. Some experimental work with centrifuging developing organisms has shown that it is possible to misplace certain developing tissues, and thereby produce abnormal organisms. This may be of some ecological interest in suggesting that pressure, especially unequal pressures, may be important in influencing the mechanism of development and possibly in extending even to the mechanism of heredity as concerned with genes on chromosomes.

The behavior of insects is undoubtedly affected by pressure, especially as concerned with reactions to gravity. It is common knowledge that many insects are negatively geotropic, i.e., that they react negatively to gravity and crawl upwards on various surfaces.

Loeb (1918), Kanda (1914 and 1916), and others have given attention to the reactions of organisms to pressure. It will not be the purpose at the present time to go into the details of the behavior of organisms, and to discuss the merits of the various views relative to these reactions.

Fielde and Parker (1904) concluded that ants did not react to aerial vibrations, but only to those transmitted to them by the substratum upon which they were resting. They concluded also from their experiments that the reactions did not depend upon the antennae, the head, the abdomen, or any pair or two pairs of legs, but that the organism as a whole reacted and that the stimulus was probably received through the legs. This was in accordance with the belief of Cole (1917), that *Drosophila* reacted to gravity because of the stress of the body as it rested upon the legs, rather than to any chordatinal organs, as suggested by Loeb. The various reactions of contact to vibrations and to pressure might logically be considered under this head. Since, however, it is not the purpose to enter into purely behavioristic or physiological phenomena, they will not be taken up further at this point.

It is difficult to correlate the effect of pressure upon the geographic distribution of insects from our present knowledge. The conclusions of Dodds and Hisaw have already been referred to as showing that altitudinal distribution may be more closely correlated with temperature than with pressure. This would seem to be reasonable, for it is certainly shown by experimental work that insects are able to endure far greater variations of barometric pressure than are ordinarily to be found on the surface of the earth.

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MOVEMENTS OF THE MEDIA

The movements of the environmental medium, especially the currents of atmosphere and of water, have profound effects upon the distribution of the organisms and upon their immediate environment. The ocean currents affect the temperature of the continents; the prevailing winds influence both the temperature and precipitation of areas, making some favorable and others unfavorable for plants and animals. In the study of autecology, we are most concerned with the effects of the currents of water and atmosphere upon the individual organisms. The effect of the currents of the ocean and of fresh water has attracted much more attention than has the study of the effects of movements of air. We are just beginning to be aware of the great effect which wind has in distributing many of the smaller organisms over the surface of the earth. We now know that the air, like the water, has a great floating population.

Methods of Measuring Currents of Atmosphere and Water.—The measurement of wind is most commonly accomplished by the use of a Robinson cup anemometer (Marvin, 1907; and Humphreys, 1920). Hemispherical cups are mounted on horizontal spokes of a wheel. The open side of the hemisphere will thus face the wind on one side, and the convex side of the cup will be directed toward the wind on the other. The instrument is connected with a recording device, which reads the

number of miles of wind which have passed over a period of time. This type of anemometer is not affected by the direction of the wind, but is clumsy to use in the field. The Buram portable anemometer consists of a four-inch fan connected with the dial, which records the passage of wind. It is equipped with a device for starting, stopping, and zero setting. The operator, however, must face it into the wind, as there is no wind vane on it. A watch is used to measure the time. It is, however, a very convenient field instrument.

The pitot tube (Rowse, 1913) may be used for measuring currents of water and also for measuring the speed of air in passing through experimental chambers in laboratory work. This instrument consists of a tube with a dynamic opening facing the wind or water current, and one or more static openings at right angles to it. The dynamic opening is connected with one side of a manometer, and the static opening with the other side. Water may be used as the indicator fluid to show that the difference of level in the two sides of the manometer will be proportionate to the rate of flow. A chart is provided, which is calibrated for either air or water, and from which the rate may be taken when the manometer reading is known. Various instruments have been devised for measuring water currents in the ocean and in large bodies of water. These will be referred to under the subject of Aquatic Synecology. For ordinary aquatic field work and for laboratory work the use of the pitot tube is one of the most convenient methods.

Movements of the Media as Factors in Animal Ecology.—For the present purpose, the action of the wind primarily will be considered under this heading. The action of the currents of water will be referred to in connection with aquatic environments in the section on synecology. Attention has already been called to the importance of wind action as affecting evaporation. Its general effect on the conduction of heat is too well known to require further attention. In all restricted environments, it is of great importance in accelerating the diffusion of gases. There are doubtless many other effects which might be dwelt upon; but in the present treatment of the subject it seems more profitable to consider the cases of distribution of organisms.

The Effect of Wind and Currents of Water on the Distribution of Animals.—The atmospheric air is in almost constant movement horizontally and vertically, on account of differences of temperature and of barometric pressure. In some cases these movements are relatively local and of short duration, while in other cases they are of great magnitude and almost continual. Humphreys (1920) calls attention to certain areas of the world where violent winds blow almost continually because of great differences of altitude, temperature, and barometric pressure. It is only within recent years that we have come to appreciate the great significance of these movements of the air in the distribution of many

of the smaller organisms. Spores of fungi have been found at an altitude of 11,000 feet.

Burgess (1913) and Collins (1915 and 1917) studied the distribution of the gipsy-moth larvae by the wind. The first instar larvae of this moth have long been known to have specialized hairs which greatly increase their surface ratio. When the surface-weight ratio of these tiny larvae is compared with that of certain seeds of plants which are known to soar in the air, it is found that they rank among the best, so far as soaring coefficient is concerned. It is difficult to get an exact measurement of the surface area; but after the first molt the long hairs are no longer present, and the larva is much less subject to transportation by the wind. When its food is scarce during the early larval life, the caterpillar lifts the anterior part of the body in an effort to find new foliage and is thereby exposed to the action of the wind. Collins studied the distribution of these larvae by putting out screens covered with adhesive. It was found that they were carried across Cape Cod Bay a distance of 19 to 30 miles; and horizontal screens placed upon meadows showed that large numbers of the larvae were being dropped on every acre of land. Reports from vessels at sea have often recorded insects being found thousands of miles from the shore.

Hurd (1917) records that swarms of grasshoppers were found 1,200 nautical miles at sea, and McCook (1890) states that spiders have been found at a height of from 1,000 to 2,000 feet in the air and 200 miles at sea.

Quayle (1916) showed that the young of the black scale, *Saissetia oleae*, were distributed by the wind from one block of trees in an orchard to another.

Felt (1925) made a study of the distribution of insects by wind in New York State, and used small balloons as an index of the direction and velocity of the winds at various times during the growing season. He states that swarms of mosquitoes have been observed at altitudes of 2,000 and 3,000 feet. Balloons which were used in these experiments, when inflated for a minimum of buoyancy, were carried by upward currents of the air to elevations of 1,000 feet. The average velocity of these drifting balloons was approximately 17 miles an hour; but there is a possibility of a speed of 50, 75, or even 100 miles an hour. Many of these balloons drifted several hundred miles in a period of 24 hours. From the records of southern insects that have been captured far in the north, it seems certain that it is not uncommon for insects to be carried hundreds or even thousands of miles by the wind. Felt reports *Alabama argillacea* as occurring in Canada, when it is known that it does not breed farther north than in the cotton regions.

Light-trap experiments at the University of Minnesota and in Montana have shown that there are many adult insects which are found

at times in the north even though their food plant is at least as far south as the cotton belt.

Elton (1925) reports large numbers of aphids, *Dilachmus piceae*, and a hover fly, *Syrphus ribesii*, which were found after a strong wind in Northeastland, Spitzbergen. These were found all over fresh snow, which indicated that they had recently arrived; and he concluded that they must have been carried by the wind at least 800 miles.

Wadley (1928, unpublished thesis) reports that the green bug, *Toxoptera graminum*, which arrived in Minnesota in 1926, must have been carried by the wind from Oklahoma. This would have required, approximately three days of continuous wind with a rate of 200 to 600 miles per day. He tabulated the wind rates from this direction during the spring of the year, and found that in 1918 and 1926 there was sufficient wind to account for such a distribution of the aphids.

At the present time we know very little of the fauna of the upper air. There are, however, several investigations under way at the present time; and doubtless in the near future we shall have more information with regard to the organisms which might be termed the plankton of the air.

This suggests many interesting problems. The limitations of the gas are not very great until a very high altitude has been reached, as has already been referred to. There is, however, a decrease of temperature at a relatively uniform rate of 6° per 1,000 m. from sea-level, to 11,000 m. where the temperature is constant at -55°C . At an altitude of 1,200 or 1,300 m., therefore, the temperature will approach 0°C . The vapor pressure of water also drops off rather rapidly and is reduced by about 20 per cent at 1,000 m. The upper atmosphere is, therefore, not a very favorable environment.

The morphology of animals is probably affected by movements of the medium in much the same way as sessile plants are affected. The pines growing along the seashore, which have been permanently bent by the action of the prevailing wind, are a classical example. We have not many sessile animals, however, which are comparable to these plants. Many aquatic organisms which swim rapidly through the water or which maintain themselves in a constant position in a rapid stream of water have a so-called "streamline form," which seems to offer the least possible resistance to the action of the current.

Clemens (1917) experimented with masses of wax which were molded into different forms, and found that when the wax was molded in the form of a brook trout, it gave a pull of six grams in a constant stream of water; whereas the same quantity of wax in the form of a cone with its apex upstream gave a pull of 50 g. A model of the may-fly, *Chironetes*, gave a pull of nine grams. There is nothing to show that the form of these organisms was influenced by the current, but rather that,

through selection, the forms living in the rapidly flowing water have body shapes which offer the minimum of resistance. Experiments in aeronautical engineering in connection with aviation have shown that this streamline form offers the minimum amount of resistance to the air. It may be noted that the bodies of the birds of swiftest flight conform more or less to this same streamline form.

Effects of Movements of the Medium on the Behavior of Animals

Wheeler (1899) observed that some of the Syrphidae (hover flies) oriented themselves to face against a slight breeze and maintained an almost constant position. To this phenomenon he gave the term "anemotropism." There is in this case, however, nothing to indicate that the organism was reacting to the pressure of the air or the movement of the air. It is entirely possible that they were reacting as a result of vision and a sense of relative position. In the case of rheotaxis of aquatic organisms, it is quite clear, in certain cases at least, that the reaction in heading upstream is due to their sense of relative position rather than to a reaction to the current of the water itself. This may be tested in the case of certain fishes by placing them in an aquarium with scenery on each side, which may be moved in one direction. When the scenery is moved, the fish turns to face the direction in which the scenery is moving and swims to maintain his relative position with regard to the scenery.

Allee (1914) has pointed out the ecological importance of the rheotactic reactions of certain stream isopods. The subject matter, however, of the detailed relationships of these organisms to movements of the medium resolves itself into a study of animal behavior of physiological nature.

Lutz (1927) found that the number of insects collected at a light on a side upwind and on the side which was downwind bore a rather consistent relationship. Only about 7 per cent of the total catch was on the windward side, and over 25 per cent was on the leeward side. This must be interpreted as the effect of wind upon the ability of insects to alight, rather than as the effect of wind on the reactions of insects. Many of them undoubtedly are carried beyond the light by the action of the wind, and then return upwind to the trap.

This discussion comes to a close with these fragmentary accounts of the effect of movements of the media. Other references will be found in connection with descriptive synecology, particularly with regard to aquatic environments.

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THE GASEOUS CONSTITUENTS OF THE MEDIA

The earth is surrounded by an envelope of atmosphere which is relatively uniform near the surface, showing very little change in altitude over a distance covered normally by organisms, and which does not vary greatly from pole to pole, as shown by the following figure taken from Humphreys (1920). In general, the gaseous constituents of various special media, such as soil, water, and others, are in equilibrium with the atmosphere. There are, however, many special restricted environments in which the gases may be present in very limited quan-

ties; and it is into these special limited environments that organisms are often forced by extreme competition which they have to meet. Oxygen and nitrogen appear to be the main constituents of the earth's atmosphere, and it would appear that no others are present in enough quantity to deserve consideration. However, carbon dioxide is very important, for all animals must rid themselves of it; and it is possible that this gas may poison them, even when there is plenty of oxygen present. The vertical distribution of gases in the earth's atmosphere is such that other factors than the lack of oxygen begin to operate before the oxygen has been appreciably reduced. Referring to the discussion upon pressure,

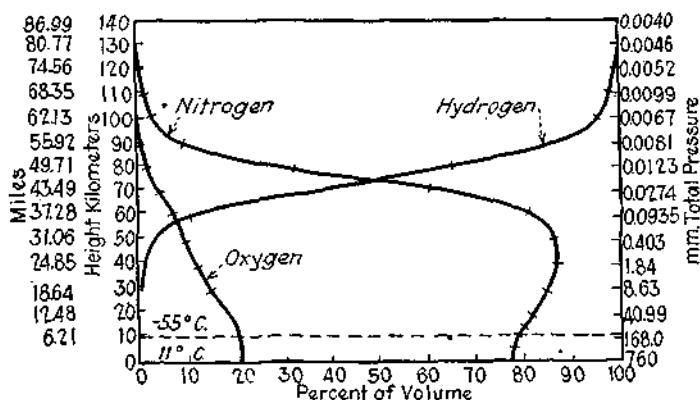


FIG. 53.—The distribution of gases in altitude. (Humphreys, 1920.)

it will be noted that the highest point reached by sounding balloons is about the point where oxygen begins to drop off appreciably. Further, temperature approaches a constant value of $-55^{\circ}\text{C}.$ before oxygen has been reduced more than half its value. Consequently, it may be seen that the immediate atmosphere of the earth is everywhere relatively favorable for insect life.

Methods of Measuring the Gases of the Medium.—The methods of measuring the quantity of various gases present in the atmosphere, and the pressure of these various gases may be found in the literature of physiology. Carbon dioxide is normally measured by the use of barium hydroxide as an indicator, and by taking the formation of barium carbonate, which is of milky color, as an index of the presence of carbon dioxide. Various devices have been constructed for measuring carbon dioxide and are described by Thunberg (1905), Lund (1919), Krogh (1919), Fink (1925), and others. The technique of obtaining a fair sample of the gas to be analyzed is important, and must be adjusted to the problem which is in hand.

GASES AS FACTORS IN THE ECOLOGY OF ANIMALS

Effects of Gases on Physical and Chemical Processes.—Oxidation is probably one of the most fundamental phenomena of biotic systems. It is naturally affected by the oxygen. If oxygen is absent, oxidation cannot go on. It may happen that some other gas is present which may combine with the oxygen, and therefore make the oxygen unavailable for a certain reaction, which is the object of investigation. Therefore, in the study of gases we come very close in our biological work to the purely chemical reactions of oxidation, which may occur in any physical system.

The Effects of Gases in the Ecology of Insects on Rates of Biological Processes.—The general requirement of oxygen for respiration is so well established that it will be considered only for the purpose of showing that it is another example of a physical factor which may be present in a minimum amount, which will produce normal activities, or in a maximum amount, which may cause death. Even the greatest necessity of life may be so abundant that it becomes toxic, or so scarce as to be a limiting factor in life. Insects, in general, have adjusted themselves to take advantage of practically every environmental niche which may be inhabited, and they have shown very ingenious adaptation to take advantage of special environments so far as the gaseous constituents of the media are concerned.

Dendy (1919) and Dendy and Elkington (1918) have shown that granary weevils are very definitely limited by the oxygen supply. This is in accordance with our general information. Lund (1921) showed that the flatworm, *Planaria*, was definitely limited by about one-third of the normal saturation of oxygen in water. The experiments of Back and Cotton (1925) with a vacuum tend to indicate that the insects died of oxygen starvation because of the fact that they were able to endure low atmospheric pressure over such long periods of time.

Bodine (1928) has shown that it is possible for insects to endure a paucity of oxygen for a period of time during which a debt of oxygen is built up in the body; but this debt is quickly made up when they return to a normal oxygen. Such conditions can be endured only as emergencies, however, and a long period would end in death. The experiments of Cleveland (1925) have given a much clearer conception of the ranges within which insects are able to endure changes in oxygen pressure. He found that it was possible to kill the protozoan symbionts in the digestive tracts of certain insects by raising the oxygen pressure. He found that high oxygen pressure was over 67 times as toxic for the protozoa as for the hosts. It seemed in this case that it was the oxygen pressure which was operating, for he found that the effect of five atmospheres of ordinary air was the same as the effect of one atmosphere of pure oxygen, which means that in either case the same pressure of oxygen was experi-

enced. The accompanying table shows some interesting relationships to oxygen pressure on symbionts and hosts. It will be noticed that the cockroach was able to endure three and one-half atmospheres of oxygen for twice as long as *Termopsis*, and many times as long as any of the internal symbionts. This seems to indicate that the oxygen tension in the digestive tracts where these parasites normally live must be relatively constant, since the symbionts themselves are so susceptible to oxygen change.

TABLE IX.—THE TIME REQUIRED TO KILL CERTAIN ANIMALS AT VARIOUS PRESSURES OF OXYGEN¹

Pressure in atmospheres	Time to kill all intestinal protozoa of										To kill trichomonas in culture from			To kill host		
	Termites								Cockroach	Frog	Frog	Rat	Man	Termopsis	Cockroach	Frog
	Rhinotermitidae				Kalotermitidae											
	Leucotermes		Reticulitermes		Termopsis		Cryptotermes									
	Hr.	Min.	Hr.	Min.	Hr.	Min.	Hr.	Min.	Hr.	Hr.	Hr.	Hr.	Hr.	Hr.	Hr.	
1.0	24				72											
1.5	4	30			9		7	30								
2.0	1	35	4		5		4	30								
2.5	1	15	1	40	2		1	55								
3.0		50		50	1	5	1									
3.5		30		30		40		35	3½	28	6	10	11	45	90	65

¹ CLEVELAND, 1925.

² Not killed in 10 days.

Cole (1921) experimented with chironomid larvae which were found in the bottom of Lake Mendota, Wisconsin, where the oxygen content of the water for several months of each year is so low that no free oxygen can be detected. The interesting problem as to how the fauna which lives in this environment is able to obtain its oxygen has not been satisfactorily solved. Cole found evidence that some oxidizing material was present, and that this presumably was atomic oxygen; and it was his conclusion that this atomic oxygen must be taken advantage of by the insects living there. Insects, in general, seem to have solved very successfully the problem of making the atmosphere accessible to their tissues.

Lee (1929) gives a good summary of the information on the respiratory mechanism of insects. It seems to be rather generally accepted at the

present time that part of the spiracles serve for the inspiratory movement of the air, and another portion of the spiracles for the expiratory movement of air. It seems rather clear, therefore, that the carbon dioxide is forced out of the body and then atmospheric air drawn in. If this is true, the reasoning of Portier (1928) might be used for concluding that the insects would usually have a higher oxygen-tension difference between their tissues and the surrounding air than would other animals; for the air would not be mixed with the carbon dioxide, but would come in as free atmospheric air almost directly in contact with the tissues themselves.

The discussion thus far has dealt very largely with oxygen, but the importance of carbon dioxide must not be overlooked. Haldane (1917) says that there may be plenty of oxygen present, but carbon dioxide may exert its toxic effect nevertheless.

Dendy (1919) showed that while it might be partly lack of oxygen that interfered with the metabolism of insects in air-tight spaces, it was very largely the accumulation of carbon dioxide. The respiratory problems of various special environments involve not only oxygen and carbon dioxide, but even nitrogen. In the case of the respiration of aquatic insects, which will be further considered in connection with synecology, Ege (1915) and others have shown that the bubble of air which is carried below the surface of the water by the insect acts as a mechanism for obtaining oxygen from the water. Since this bubble ordinarily contains four-fifths of its volume in nitrogen, and only one-fifth oxygen, the nitrogen becomes the important factor. As the insect begins to consume the oxygen, the carbon dioxide which is given off diffuses into the water so rapidly that Ege did not take it into account. As oxygen consumption proceeds, the oxygen pressure in the bubble is decreased, and the nitrogen pressure is relatively increased. If we assume that the bubble was in equilibrium with the gas in the water at the start, this change of pressure will lead to a diffusion of oxygen into the bubble and of nitrogen out of the bubble. Since the bubble will continue to exist and act as an air supply until both gases are entirely gone, it is important to know their relative rates of diffusion. Ege compared the rates by the use of a formula and concluded that the oxygen diffused into the bubble over three times as rapidly as the nitrogen passed out. Consequently, the amount of oxygen which would be available from the bubble mechanism would be about 13 times the amount that the bubble originally contained. This applies, of course, to adult insects, which carry bubbles of air below the surface of the water. Nearly all aquatic insect larvae, especially those of the *Diptera*, respire by means of surface respiration and tend to keep the gases in solution in their bodies in equilibrium with those which are in solution in the water.

There are many problems of respiration in special environments of the soil, decaying animal bodies and plant material, which are of special interest to the ecologist, and which require special investigation.

Effects of Gases on the Morphology of Animals.—Here, as in other cases, it is necessary to discriminate between established relationships and assumptions based upon general observations. Purely physiological considerations of conditions which are not known to exist in nature may also be omitted.

Gerould (1924) called attention to the effect of oxygen and temperature in the formation of melanin in the wings of *Colias*. In some experiments he tried shutting off the oxygen supply in certain areas of the wings which developed melanin. He found, however, that his method did not inhibit the formation of the melanin. His general conclusion is that melanin is formed when metabolism is slowed down, whatever the cause of the slowing may be. It is nevertheless true, however, that oxygen is required for the reaction, as he pointed out.

We might conclude that where oxygen is required for the reaction in pigment formation, its absence from the environment would affect color. Further experimentation is required before we shall be able to draw definite conclusions.

Effects of Gases on the Distribution of Animals.—It has already been pointed out that over the various areas of the earth there is very little change in the constitution of the atmosphere. Therefore, we would not expect that the geographic distribution of animals would be greatly affected by the gases of the atmosphere. However, certain local distributions may be very profoundly affected. This is shown to be true in the case of fresh-water lakes and the case of the organisms living in the bottom where oxygen is low or absent, as has already been referred to. It may also be an important factor in the distribution of animals in the soil, as will be taken up under the subject of Synecology. It would seem in general that the distribution of gases and respiration was largely a physiological problem, rather than an ecological one.

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NEUTRALITY OF THE MEDIA

The neutrality of various media explored from the point of view of hydrogen-ion concentration serves as one of the best examples of a rush of scientific workers into a new field. In 1920 Clark published

his first edition on the measurement of hydrogen-ion concentration. In eight years this has been followed by a series of reprints and new editions, until at present we have a volume which is more than twice the size of the original edition. In the introduction to the last edition Clark (1928) called attention to the fact that the number of papers occurring on hydrogen-ion concentration up to 1918 hardly reached the point of 100 per year. In 1927, almost 1,500 papers on this subject were published.

Several factors apparently have contributed to the great popularity of this field. The physiological importance of dissociated ions has been clearly demonstrated. A convenient method of measuring and expressing concentration is available. And last but not least, it has opened up a field in which new facts can be obtained very quickly with very little effort, and there is a great possibility of significance being attached to them. It would be extremely presumptuous in a volume of this nature, with one chapter devoted to the neutrality of the media, to attempt to give such a presentation that the uninitiated might have a clear appreciation of hydrogen-ion concentration, together with a proper conception of its fundamental importance, and in addition to give a summary of examples of the results of the vast amount of investigation. The student is referred to Clark (1928) and to the general textbooks on physiology to form his conception of the importance of hydrogen-ion concentration.

It may be worthwhile to give a brief discussion of the fundamental factors involved in the equilibrium between acids and bases in various systems. Pure, distilled water is often taken as an example of a neutral solution. This contains both hydrogen and hydroxyl ions in accordance with the following formula: $\text{HOH} = \text{H}^+ + \text{OH}^-$. This means that dissociated ions of hydrogen carrying a positive charge may be found free in the water, and that hydroxyl ions carrying a negative charge may also be found. In the case of distilled water, we have a neutral condition, and the system is in equilibrium. This is formally expressed with this

equation, $\frac{[\text{H}^+][\text{OH}^-]}{\text{HOH}} = K$, in which the dissociated ions are indicated in

the numerator, and the undissociated residue in the denominator. As a matter of fact, in the case of distilled water there are so few dissociated ions that the denominator of this fraction may be disregarded for practical purposes. In the case of acid solutions the "strength" of the acid is due to the dissociated ions, which act as electrolytes. Consequently, two acids present in the same per cent of normal solution may have different "strengths" since there are more dissociated ions in the stronger of the two acids. Hydrochloric acid, for instance, is about 90 per cent dissociated in one-tenth of one per cent normal solution. Acetic acid is

about 1.3 per cent dissociated in a tenth normal solution. Consequently, we speak of hydrochloric acid as being much "stronger" than acetic acid.

What has been said of acid solutions might also be said of alkaline solutions. In the case of acid solutions, we were speaking of the hydrogen ions; and in the case of alkaline solutions, of hydroxyl ions. Consequently, the acidity, the alkalinity, and the neutrality of a medium will depend upon the balance of the dissociated hydrogen and hydroxyl ions.

Methods of Measuring the Concentration of Ions for Ecological Work. Much of the progress which has been made in biological studies on the effect of neutrality, acidity, and alkalinity has been due to the introduction of new methods of measurement and quite largely to new methods of expression. These new methods have at the same time advantages and disadvantages. The introduction of a simple system of expression has allowed biologists to neglect and even forget the fundamental conceptions upon which the expression is based.

An acid solution may be described in terms of its normality with respect to total acids or with respect to the hydrogen ions. A normal solution of acid is one which contains 1.008 g. of acidic hydrogen in a liter of solution. And a normal solution of hydrogen ions is one containing 1.008 g. of hydrogen ions per liter of solution. These two expressions of normality lead to confusion. Clark (1928) has suggested that we speak of a normal acid solution in the older sense as the "quantity" factor of acidity, and of the hydrogen-ions' normality as the "intensity" factor. It is with the activity of these hydrogen ions that we are concerned at the present time, and attention will now be turned to the expression of the concentration of these hydrogen ions.

Because of the necessity for expressing extremely small fractions of the normal value, the expression of the concentration of hydrogen ions becomes cumbersome, especially to biologists who are not accustomed to thinking in terms of mathematics. Sorensen greatly simplified the notation by adopting a system which is now known as the pH value. At the same time that the notation was simplified by this system of values, the conception of the quantity of hydrogen ions present was greatly complicated. Sorensen's expression was "the logarithm of the reciprocal of the concentration of the hydrogen ions expressed in grams per liter,"

and may be given formal expression as $\text{pH} = \log_{10} \frac{1}{[\text{H}^+]}$, or $\text{pH} = -\log_{10} \text{H}$, so that H may be written $[\text{H}^+] = 10^{-\text{pH}}$. Here the $-\text{pH}$ appears as an exponent, and the term pH literally means the power of hydrogen-ion concentration. In interpreting the pH scale, it is important to keep in mind the fact that the exponent expressing the concentration of hydrogen ions has a negative value, *e.g.*, hydrogen-ion concentration

equaling 10^{-7} normal is expressed by the pH scale as 7. The accompanying table shows the relationship between these values for hydrogen-ion concentration, the pH scale and the hydroxyl-ion concentration. The scale of hydrogen-ion concentration or pH goes from one to one one-hundredth trillion normal, whereas the pH scale goes from 1 to 14. There is an enormous advantage in this simplified scale, but a complication in understanding what pH actually means. The fact should be further emphasized that a pH value is an actual value derived from the concentration of hydrogen ions in grams per liter.

RELATIONSHIP BETWEEN VALUES FOR H-ION CONCENTRATION, AND THE OH-ION SCALE

pH	Log of H			Log of OH
1	10^{-1}	0.1	0.0000000000001	10^{-13}
2	10^{-2}	0.01	0.000000000001	10^{-12}
3	10^{-3}	0.001	0.00000000001	10^{-11}
4	10^{-4}	0.0001	0.0000000001	10^{-10}
5	10^{-5}	0.00001	0.000000001	10^{-9}
6	10^{-6}	0.000001	0.00000001	10^{-8}
7	10^{-7}	0.0000001	0.0000001	10^{-7}
8	10^{-8}	0.00000001	0.000001	10^{-6}
9	10^{-9}	0.000000001	0.00001	10^{-5}
10	10^{-10}	0.0000000001	0.0001	10^{-4}
11	10^{-11}	0.00000000001	0.001	10^{-3}
12	10^{-12}	0.000000000001	0.01	10^{-2}
13	10^{-13}	0.0000000000001	0.1	10^{-1}
14	10^{-14}	0.00000000000001	1.0	10^{-0}

There is an interesting buffer action of weak acids and their alkali salts, which tends to resist changes in the concentration of ions about the neutral point. When an alkaline solution is added to an acid solution to neutralize it, the ions which were originally undissociated tend to become ionized to maintain the original condition. Thus a solution which is near the neutral point tends to resist any change by dissociating ions to maintain its original ratio of hydrogen and hydroxyl ions. This process is very important in protecting organisms against sudden changes in hydrogen-ion concentration. Henderson (1913) has stressed this point as illustrating how environments tend to adjust themselves to present the conditions most desirable for organisms.

For methods of determining the hydrogen-ion concentration of solutions the student is referred to Clark (1928). There are a number of outfits for field work which use both the colorimetric and electrometric methods of determination. These make it possible to take field readings with very little apparatus and in a short period of time.

Neutrality of the Medium as a Factor in the Ecology of Animals.—The neutrality of the medium is of particular importance in the ecology of aquatic and soil-inhabiting animals. For this reason its significance will be taken up under the chapters on Synecology, which discuss

the various environments in which it is concerned. At the present time, attention will be called only to its general ecological importance. Inasmuch as neutrality itself is a condition of equilibrium between the dissociated hydrogen and hydroxyl ions, the conclusion follows that it may be influenced by many of the environmental conditions. Consequently, the hydrogen-ion concentration of a given environment may be looked upon as a sort of a "symptom" rather than a "cause" of any particular condition in the environment. It is very difficult to evaluate any relationship between pH and the environmental conditions. Therefore, it is necessary to look upon the pH value as a sort of algebraic sum of the general condition of the environment rather than as a definite measure of some causal factor.

Effect of Hydrogen-ion Concentration on Physical Processes.—Much of the importance of the hydrogen and hydroxyl ions may be due to their ability to carry electrical charges. The recent literature seems to indicate that many physical phenomena are influenced by these electrical charges, and that very small changes in hydrogen-ion concentration may result in very significant changes in the physical properties of substances, all of which may enter into the functioning of the animal mechanism. The quadrivalent thorium ion is said to be capable of reducing the surface charge of quartz by 50 per cent when it is present in the concentration of only one gram ion in a thousand million grams of water. It is such surprising results as these that have led the great number of investigators to turn to the hydrogen ion as the cause of all sorts of natural phenomena. The index of Clark's most recent edition will lead to a great deal of information on these phenomena.

General Effects of the Concentration of Hydrogen Ions upon Animals.—The sensitiveness of the animal mechanism to changes in the concentration of hydrogen ions is becoming a classic example of the importance of physical factors in animal physiology. It is stated that an addition of 0.00004 per cent solution of hydrochloric acid in the circulating blood of a frog is sufficient to kill the heart. The respiratory center and other tissues are apparently just as susceptible to changes in hydrogen-ion concentration. The permeability of membranes is very markedly affected also by changes in hydrogen-ion concentration. The modern textbooks of physiology are filled with examples, and almost daily new papers are coming into print showing additional effects of changes of hydrogen-ion concentration.

Considering the hydrogen-ion concentration as a physical factor of an environment, it may be compared with the other physical factors which, in general, have some optimum concentration for the existence of animals with a pessimum lying at either side. With all the study which has been devoted to pH in recent years, there are still few authentic cases in which the optimum hydrogen-ion concentration has been definitely demon-

strated and where the curves dropping off to the pessimum on either side have been critically marked out. It seems probable that in some organisms such zones of optimum and pessimum may be demonstrated, while other organisms may possibly be able to tolerate great extremes of hydrogen-ion concentration because of either a buffering action of the organism or a great resistance to actual change of hydrogen-ion concentration.

Arrhenius (1921) found that the optimum pH for the survival of earthworms in potted soil was a pH of 7. Above and below this point, the worms died in a shorter period of time. Saunders (1924) found that protozoan, *Spirostomum ambiguum*, was most active at the pH of 7.4, but died at a pH of 8. It had its activity greatly reduced by a pH of 6, though it was not killed at more acid conditions. Saunders believes that the difficulty of keeping a culture of *Spirostomum* in the laboratory has been due mainly to the inability to maintain an aquarium at the required pH rather than to the low oxygen content of the water, as has been previously supposed. Senior-White (1926) states that the neutral waters of Ceylon range from pH 5.4 to 9.2, but that the mosquito larvae, in general, range only from pH 5.8 to 8.6.

It is doubtless true that many other insects have a limiting range of hydrogen-ion concentration. Stickney (1922), however, in experimenting with the dragonfly, *Libellula pulchella*, found that it was indifferent to acidity even to a pH of 1, and lived apparently unharmed in various pH values.

Philip (1927) transferred insects from one part of a lake to another which involved a considerable change of hydrogen-ion value without any noticeable effect whatever. It is probably true in many of these cases that the organisms are capable of buffering the environment and thereby preventing their coming into direct contact with these great changes. We seem to have little dependable evidence of the effect of hydrogen-ion concentration on the rate of the metabolism and development of insects, or upon the form and structure of any of them.

Effects of the Concentration of Ions on the Behavior of Animals.—Shelford and Powers (1915), Wells (1915), Shelford (1918), and others have investigated the reaction of fishes in gradient tanks where various pH concentrations were maintained. It is stated that fish, in general, have a rather definite reaction in choosing an optimum pH, and that, in the Puget Sound region, herrings were found but once in the water above 7.9. They were never found in water below 7.71, and the greatest number were found at pH 7.76 and 7.73. Other species were found to have other optimum pH values varying between 7.98 and 8.08. However, Behre in 1925 stated that in an investigation of Pacific Slope waters, he found them to vary between pH 6.8 and 8.4, and that fish were found to be independent of a considerable variation in pH. All fish which were found in the water of pH 7, were also found in that of pH 8.4. This seems to

mean that the pH readings taken, are a measure of certain conditions existing in the environments

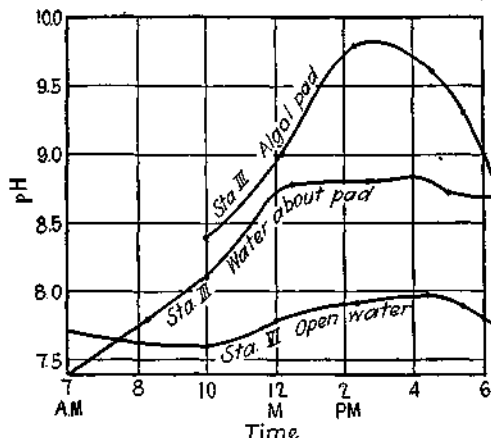


FIG. 54.—Diurnal fluctuations in pH values in Crystal Lake waters during an onshore wind. Station III in shallow water. Station VI at the "drop off." (Philip, 1927.)

which affect the equilibrium of ions, and that the organisms themselves are capable of buffering their environmental media. Consequently, it would seem that little significance could be attached to these references in literature to the effect of hydrogen-ion concentration on the distribution of organisms. Shelford (1925) called attention to the difference in hydrogen-ion-concentration readings obtained in various lakes in the western part of the United States.

However, Philip's experience (1927) seems to indicate that a series of readings with as great a variation of pH as Shelford found over the western United States could be found in a single lake even within a single day. This will be referred to later in the subject matter of Synecology.

Hall (1925) presented an interesting example of the combined effect of neutrality and oxygen. Her data, as presented in Fig. 55, furnish another interesting illustration of the combined effects of two factors varying under experimental conditions. The lines are drawn to represent equal times for the development of the short-fin rays of the whitefish. The pH values in the experiment

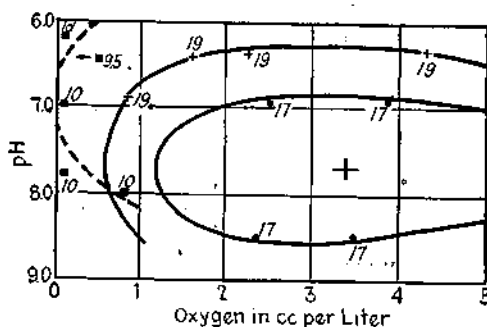


FIG. 55.—Showing equal lines on an oxygen-hydrogen-ion chart. The broken line passes approximately through combinations of oxygen and hydrogen-ion concentration in which the embryos developed a flat tail in ten days, beginning four days after spawning. The solid lines pass through combinations of oxygen and hydrogen-ion concentration in which the embryos developed short fin rays in 17 and 19 days respectively. The general trend of these lines suggests that development may be expected to be more rapid at about 3.4 cc. of oxygen and pH 7.6 to 7.7 where the large cross is placed. This cross is in the center of the ellipse. The center of the ellipse suggested by the flat-tail curve would fall at a higher hydrogen-ion concentration. (Hall, 1925.)

were controlled by CO_2 concentration. The approximate position of optimum condition for short-fin

development is indicated by the large "X" on the diagram. This seems to indicate that the changes of pH within the range shown had a greater effect on the rate of development than did the range of oxygen used in the experiment. However, it is not possible to draw a general conclusion from so few observations. We then conclude that the study of the hydrogen-ion concentration of various environments will furnish interesting supporting evidence in any complete ecological study, but that at the present time we do not have before us evidence to show that hydrogen-ion concentration is a predominant factor in the ecology of animals.

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CHAPTER VII

NUTRITION

It cannot be said that nutrition is a purely physical factor of ecology for the reason that no animal, so far as we are able to discern, is able to live upon a diet which does not contain some compounds which have been synthesized by another organism. We have therefore arrived at the point where physical autecology and biotic autecology are merged, and it is an arbitrary matter as to whether this chapter is to be included under physical autecology or biotic autecology. All animals are dependent upon at least one other organism for the preparation of their food. In fact, there has not yet been demonstrated a case in which an animal may be reared in the laboratory on a purely synthetic diet in the sense that every compound involved has been synthesized, independent of the existence of any other organism. There is probably no better example in all nature of the interdependence of organisms than that of nutrition itself.

Nutrition is a broad subject when considered in the present sense. It may be conceived of as including all organic and inorganic chemical compounds which an animal takes into its body from the environment. It includes all materials which go into the upbuilding and maintenance of the animal mechanism and is the direct source of all the energy which is used in its metabolism. From the viewpoint of biochemistry and physiology, it constitutes a great new field of biological science in which enormous progress has been made in the last few years. Its subject matter could not be adequately presented in a smaller space than a large volume. It is not possible in these pages to more than call attention to some of the important literature and to try to point out the ecological significance of the general nutritional relationships of animals.

Method of Measuring Nutrition.—The nutritional value of foods was measured in terms of calories but a short time ago. This gave a physical measurement quite comparable to those in use in connection with all the physical factors of the environment which have just been considered. Within the past few years attention has been called to certain food accessories: vitamins. These are measured only by biological tests. That is, it is necessary to feed the material to animals and note its effect upon the rate of growth, the condition of maintenance, reproduction, and general metabolism of the animal. These measures are all biotic rather than physical and are more or less relative in our present state of knowledge.

This may be considered another reason why it might be more logical to include the factor of nutrition under biotic autecology, because its measurements are all essentially biotic.

Method of Controlling the Nutritive Value of Food.—There are two methods which are generally used in experimental work on nutrition. One is to build up a synthetic food by putting together certain materials, supposedly of known composition. These combinations may be changed, and the corresponding changes in the rates of growth of the organisms noted. This method is well illustrated by the work of Sweetman and Palmer (1928). If it is possible in such work to use pure chemicals, the food requirements may be rather completely analyzed. However, it is usually possible to get no further than the use of some general plant or animal product, the composition of which may not be completely known.

The second method is to start with the normal food of the animal to be studied, and extract certain substances from the food and note the consequences. The difficulty with this method when used alone, is the ability to extract only the one material desired and leave all the others unchanged. Obviously, it is most desirable to combine the two methods of study whenever possible. Examples of the use of these methods are shown in the text in the description of various features of research.

NUTRITION AS A FACTOR IN ANIMAL ECOLOGY

There is probably no other subject under which it will be more necessary to restrict ourselves to the significance with respect to insects as compared with other animals than in the case of nutrition. The general nutritional relationships of animals are so complex, so far reaching, that we must refer to other animals only to get the proper perspectives in our consideration of the insects. In general, the literature before us is purely descriptive, tending to be mere descriptive natural history and quite neglectful of the physiological relationship.

Uvarov (1928), in his excellent consideration of insect nutrition and metabolism, says:

The first glance at the summary, and particularly at the voluminous bibliography, including nearly 600 titles may give the impression that a very large amount of work has been done on the problem of insect nutrition and metabolism, but when all the data available on these particular subjects are put together, it becomes clear that very few points have been touched and the results achieved are but a drop compared with the ocean of unknown phenomena.

In general, literature tells us upon what plants or in what media insects may be found, with the assumption that these plants and media constitute the food, and very little is said of what actually is used by the insect for food.

The Source of Energy in Physical and Chemical Processes.—In the routine treatment of each physical factor of the environment, it has

seemed well to call attention first to the action of the factor under consideration upon the physical processes, before taking up its effect upon the animal mechanism. In the case of nutrition, it would have been easier to make this comparison a few years ago when the energy balance had been worked out upon the basis of oxidation, and each animal was described as requiring a certain number of calories per unit weight of its body. In our present information about vitamins and hormones, the subject of nutrition looks more complicated than ever before. We realize that more than proteins, carbohydrates, and fats must be available in order to have a normal functioning of the animal mechanism. If we are to make the classical comparison between an organism and a machine, we must consider the general food, as we usually speak of it, as the fuel for oxidation; while the vitamins and other substances which must be present in small quantities will be comparable to the proper lubrication of the machine to keep it in running order. It is quite possible that, as we obtain new facts and get our information better correlated, the general subject will appear more simple. In the case of insects, we are probably less able to make generalizations than in the case of birds and mammals which have been the object of most of the nutritional research.

The Effect of Nutrition on Biological Processes.—Before proceeding with the ecological consideration of our information about the nutrition of insects, it will be well to get a perspective of the entire field of nutrition by considering the broader groups of organisms in their nutritional relationships. We may distinguish, in general, three great groups of organisms. We have, first of all, the photosynthetic forms which have sometimes been called "autotrophic." These are the green plants which can build up the complicated proteins, polysaccharides, and fats of their tissues from nitrates, phosphates, and sulphates from carbon dioxide and water, with the energy of sunlight. This photosynthetic power is of the greatest importance to the entire organic world; for it is by means of this process that the energy of sunlight is captured and passed on to all living organisms. We cannot conceive of the existence of the organic world, as we know it, without this one great step in nutrition.

There is a second group which is composed of microorganisms which cannot form sugar or starch from carbon dioxide, sunlight, and water, and these organisms, consequently, must be offered more complicated compounds for the synthesis of their carbohydrates. But these forms have the ability to form their proteins from an ammonium salt or a single amino acid. Certain of these microorganisms can even capture the nitrogen of the air and combine it in such a way that it can be made use of by higher organisms. This is a very important function, for available nitrogen constitutes one of the great limiting factors of all organisms. Even the autotrophic organisms must get their nitrogen in the form of nitrates.

The animals, in general, are typical of the third group. They must have their carbohydrates in the form of sugar or starch, and their nitrogen in the form of one or more proteins. These requirements stand in striking contrast to those of the photosynthetic or autotrophic organisms which are capable of capturing the energy of sunlight and combining it with carbon dioxide and water of the atmosphere; and to the second group of microorganisms which is capable of taking the nitrogen from the earth's atmosphere, and so combining it that it can form the basis for all of the protein of the living organic world. The animals, or zootrophic forms, therefore, stand considerably removed from the raw natural resources, so far as their nutrition is concerned. When we add to these requirements the list of all the vitamins required for the normal functioning of the animal mechanism, it seems even more restricted as to its nutritional requirements. There are at least five vitamins which are conservatively accepted as having been demonstrated. Some of these are so complicated that it is proposed to divide them into several factors, and there are many others that have been proposed which are not accepted by the more conservative nutritional physiologists.

We have in general the Vitamin A which is fat soluble; it is found in cod-liver oil, butter, eggs, green vegetables, and fruit. Its absence produces xerophthalmia and widespread weakening of the body. The Vitamin B which is water soluble is found in whole grains, and its absence causes the disease known as beriberi. Vitamin C is found in fresh fruits and vegetables, and its absence produces in mammals the disease known as scurvy. Vitamin D which is found in cod-liver oil as the richest source seems to be affected by the presence of sunlight. The absence of Vitamin D causes rickets and interferes with the calcium phosphorus metabolism at least in the case of vertebrates. Vitamin E is the only one which seems to be fairly abundant in the tissues of animals, and its absence causes sterility.

Our general perspective of the nutritional requirements of insects will be considered further in the general cycle of nutritional substances in nature. The nitrogen cycle has become a classical example of the history of an element in the organic system. Baumberger in 1919 modified Bayliss' diagram of the cycle of nitrogen. The dots and dashes represent the portions of the diagram which have been put in by Baumberger as the result of his investigation of the nutritional requirements of insects. This is one of the best examples of the interdependence of animals. Physiological investigations of nutrition are continually bringing new light upon the various processes involved, and raising new questions as to the limitations of the various forms that appear in the nitrogen cycle. The general scheme of things remains, however, about the same. There may be some question as to the actual restrictions of animals in capturing free nitrogen from the air; but it is, in general, true that the

number of organisms which can do this is very greatly limited, and that the entire kingdom of nature looks to relatively few for fixing all the nitrogen. Plant protein is, in general, the supply of animal protein, and animal wastes form a large portion of the source of ammonia which is acted upon by bacteria to be reduced to nitrates, and then to return again to plant protein. Baumberger has shown that the insects with the symbiotic relationship of fungi are able to short-circuit part of this great cycle. Plant and animal residue may be used more or less directly by

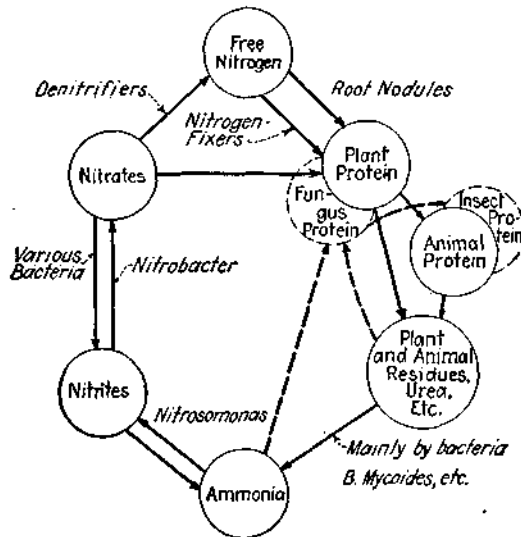


FIG. 56.—Diagram of the nitrogen cycle from the atmosphere through plants and animals. Modified from Bayliss by Baumberger to illustrate the relationship of insects to fungi.

the fungi; and the fungi, by the insect. This, however, does not make any fundamental change in the great nitrogen cycle in nature.

The carbohydrate cycle is no less fundamental than the nitrogen cycle. It is in the course of this cycle that the carbon dioxide of the atmosphere is made use of by plants, which are eaten by animals and carbon dioxide is eliminated by the animals to be returned again to circulation. The insects share the limitations of all animals in respect to these great cycles of nutritive materials in accordance with the laws of nature. For practical purposes, however, many of the insects have developed a system of exempting themselves from the direct action of some of these most stringent restrictions. They have made themselves ecologically independent of some of the physiological restrictions, by associating themselves with microorganisms, in such a way that their symbionts will make up for their own short-comings in the cycles of nitrogen and carbon dioxide. It is this ecological exemption which has led to a great deal of confusion in the description of food habits of insects. There is

hardly an organic substance in which insects have not been described as living. They have been able to invade environments of almost pure cellulose where available nitrogen and carbohydrates are not ordinarily considered to be present. They have been able to support themselves in soil and water, and in all the residues of plants and animals. The most recent investigation seems to indicate that they do most of this through their association with symbiotic microorganisms. In some cases, this symbiotic specialization has gone on to such a point that the insects are no longer capable of an independent existence. They become an inseparable part of an ecological unit just as cells in the animal organism have become an inseparable part of the organism. The individual cells may be cultured separately with the greatest care, but in nature they must live in the organism. So these insects may, when proper precautions are taken, be cultured separately from their symbionts, but so far as nature is concerned, they must always exist with them.

In considering the nutritional requirements of the insects for the maintenance of their metabolism, there may be some advantage in dividing them into groups which are classically used in literature. At the same time it must be recognized that the groups may not necessarily be valid groups, as they are based upon general observations as to what seemed to be the food requirement of the insects. When properly analyzed, these groups may be shown to be false, but they can at least form the basis for our discussion. Handlirsch (1926) indicated 29 categories of food habits of insects:

FOOD HABITS OF INSECTS

(English equivalent of Handlirsch's list)

1. No food. (Atrophic.)
2. A very special food. (Monophagous.)
3. Several kinds. (Heterophagous.)
4. Great variety—practically everything. (Pantophagous, omnivorous.)
5. Substance of animal source. (Zoophagous.)
6. Entire animals, especially meat. (Carnivorous.)
7. Prey, either killed or still living. (Predatory.)
8. Dead animals (Zoonekrophagous.)
9. Decaying animals. (Zoosaprophagous.)
10. Sucking blood, which as a rule does not kill the animal. (Haematophagous.)
11. Animal excrements. (Koprophagous.)
12. Liquid secretions, such as spittle, honeydew, etc. (Zoosuccivorous.)
13. Other animal waste, parts of integuments; scales, hair, feathers, wax, silk, etc. (Detritivorous.)
14. On or in a living animal, or its body substances without killing immediately or in fact not killing at all, and staying on or in the host continually, a life time, or at least a long time in one stage. (Ecto- and Endo-parasitic.)
15. Eating each other. (Cannibalistic.)
16. Substance of plant origin. (Phytophagous.)
17. Living plant parts. (Herbivorous.)

18. Algae. (Algophagous.)
19. Lichen. (Lichenophagous.)
20. Fungus. (Mycetophagous.)
21. Woody plant parts. (Xylophagous.)
22. Fruits and seeds. (Carpophagous.)
23. Pollen. (Pollenophagous.)
24. Honey. (Melliphagous.)
25. Other plant saps. (Phyto-succivorous.)
26. Dead plant substances. (Nekrophytophagous.)
27. Decaying plants. (Saprophytophagous.)
28. In galls. (Gallivorous.)
29. Soil. (Geophagous.)

For the sake of the present discussion, we will recognize the phytophagous forms, or plant feeders; saprophagous, or those feeding upon decaying or fermenting organic substances; harpactophagous, or predatory, forms which might also be called carnivorous insects. We might also recognize parasitic forms. These would be distinguished from the predatory in that they inhabit but one host during their life cycle. However, this distinction seems to be of relatively little importance for our present consideration. These categories may be readily harmonized with the physiology of nutrition as may be seen by noting the position they would occupy upon the nitrogen cycle. More of them are associated with plants than with any other form of food as might be expected, for this is the source of the basic food supply for all organisms.

Weiss (1926 and other papers) has made a study of the number of species found, having the various food habits. This is a sort of a qualitative measure as we have no right to assume that the number of individuals is directly proportional to the number of species. However, he found in general that about half the species were phytophagous; about 25 per cent of them, saprophagous; about 15 per cent harpactophagous; and about 10 per cent, parasitic. Table X gives the comparison of the number of species in these various categories in different parts of America;

TABLE X.—COMPARISON OF THE NUMBER OF SPECIES IN THESE VARIOUS CATEGORIES IN DIFFERENT PARTS OF AMERICA¹

Habitat	Total species considered	Phytophagous, per cent	Saprophagous, per cent	Harpactophagous, per cent	Parasitic, per cent	Pollen feeders, misc. species, per cent
Atlantic coast of North America....	423	45	26	14	11	4
West arctic of North America.....	402	47	27	14	10	2
State of New Jersey.....	10,500	49	19	16	12	4
State of Connecticut.....	6,781	52	19	16	10	3

¹ WEISS, 1926.

and it is interesting to note how consistent were the results which Weiss obtained. This seems to indicate that the further removed a species is from the source of food supply, the smaller the number of species will be. This is not consistent with the conclusion of Stunkard (1929), who considered that there were more species of parasites than of all other animals together. He arrived at this conclusion by considering that each species of animal has one or more parasites.

Phytophagous forms vary greatly in their nutritional requirements and may differ as to the choice of host, and the choice of the part of a host. Some insects will eat the foliage of almost any plant, as Japanese beetles, certain grasshoppers, and others do. There are others which are restricted to one species of plant. They will not feed upon any other species, nor can they develop if forced to feed upon another species. There are still others which have a range of host plants but which when started upon one species will not accept one of the alternate food species; but must complete their development upon a species on which they originally started. In some cases the selection of the host-plant is made by the female when she deposits her eggs upon the species on which the larvae are to feed. In other cases the larvae make their own selection. There is much of interest to be found in the study of the selection of food plants. Brues (1924, and in other papers) has given consideration to this subject. Craighead (1921) and others have concluded that when a species has been reared for several generations on one of several alternative host plants, the progeny will tend to select the same host plant on which they were reared.¹ There are several possibilities in this connection. It is entirely possible that there may be various strains of each species, some strains feeding upon one host, and other strains feeding upon other host plants. It is also possible that in any given species there may be many heterozygous strains with all the possible combinations of host-plant preferences. If this is the case, there may be a selective action of the environment in eliminating all of the progeny which have a tendency to choose other host plants than those upon which they hatch. This would lead to the progeny which survive choosing again the same host plant on which they were reared. Thorpe (1929) experimented with the small ermine moth, *Hyponomeuta padella* L., which feeds on apple and hawthorn. He concluded from biological, genetic, and morphological evidence that there are two or more biological races within a single species. When the "hawthorn form" was placed on hawthorn and apple, 911 eggs were laid on hawthorn, and 237 on apple in three experiments. When those of the "apple form" were given their choice, 367 eggs were laid on hawthorn and buckthorn, and 3,395 on apple. Thorpe thinks that it is possible that this is an example of an induced situation.

¹ This is sometimes called the "host selection principle."

Every organ of a plant may serve as an environment for an insect. Some species are so closely restricted that they are present only in galls upon flowers, as for instance the famous gall of the oak, which is restricted in its environment not only to a certain species of oak but to the stamens which are present during a few weeks of the year. The physiological conditions represented by these various environments even within a single plant differ greatly. Hering (1926) called attention to the fact that the nutritive value of the different parts of the leaf may vary greatly. In the extensive work done upon the nutrition of silkworms, it has been shown that the nutrition of the leaves varies from one time of day to another depending upon whether the contents are essentially starchy or higher in proteins.

Portier (1905) found that the caterpillar, *Nepticula*, which lives on the parenchyma tissue of rose leaves was surrounded by sterile conditions. Baumberger (1919) investigated large numbers of cases of *Prothertri dispar* and found all but a few pathological cases to be sterile. However, the larvae of *Nonagria typhae* which lives in the trunk of the cat-tail, *Typha latifolia*, lives in a symbiotic relationship with a micrococcus and a fungus. It seems possible, therefore, that many supposedly phytophagous forms feeding upon green plants are actually living in symbiosis with microorganisms. It seems in general that those forms which live in closed burrows in growing leaves live under sterile conditions; while those forms which live more or less exposed may be associated with microorganisms. Many questions may well be raised with regard to the nutrition of foliage feeders.

Davidson (1923) has concluded that, in the case of the aphids, more attention should be given to the nitrogen requirement. Most of the sap which the aphids draw from the leaves consists of carbohydrates; but he points out that the aphids excrete large quantities of honeydew or carbohydrates. This is probably done during the time that they are concentrating their nitrogen. The nutrient solutions to which the plants have access, undoubtedly affect the organisms feeding upon the leaves. Uvarov suggests that plants may be protected from aphids by the use of acid fertilizers; also Müller (1926) suggests that aluminum sulphate and paraffin solution will keep aphids off the plants if it can be tolerated by the plants, i.e., if it is not injurious. Or we may spray the leaves with nutritive materials in much the same way as we now cover them with poison to kill insects. This would seem to be a fertile field for investigation.

Turning our attention next to the insects which live in the supporting structures, we have the group which is referred to as xylophagous. These insects live in the portion of the plant which is relatively high in carbohydrates and low in protein. Haberlandt (1915) concluded that the digestibility of wood was very low and that unless cellulose is changed or

destroyed, it has little food value for animals. General observations lead to the conclusion that most insects which live in wood are long-lived. It would seem from this that it requires the ingestion of large quantities of wood in order to accumulate enough protein and other essential materials to complete development. Hubbard (1897), Neger (1908), and many others have shown that most of the insects which apparently feed only upon wood are, in fact, associated with fungi and other microorganisms. The most convincing and complete evidence we have upon this subject is from Cleveland (1923 and 1928) who has studied the symbionts in the intestine of the termites. He states that in some cases half the weight of an adult termite may be due to the protozoan symbionts without which it is unable to live.

It was experimentally demonstrated that when these termites were deprived of their symbionts they could not live on their normal food of cellulose. The symbionts were removed by three methods: by high pressure of gases, by heat, and by starvation. In all cases the results were the same. The six control animals which continued to feed on wood lived normally; while those which were deprived of the protozoan symbiont were unable to live. He found further that all termites which fed upon wood contained these protozoan symbionts. In certain species there are casts which do not possess the symbionts; and these are obliged to feed upon the salivary secretions, or the excrements of the ones which do have the symbionts in order to maintain themselves, even though they continue to feed upon the wood. There seems to be no doubt, after the studies made, both of the termites and their symbionts, that the symbionts digest the cellulose and make it available for the termites. It does not answer the question, however, with regard to how the nitrogen is made available. Heitz (1927) studied a large series of wood-feeding insects and demonstrated that there were symbionts present in all of them, either bacterial or protozoan. In some cases, he found special portions of the digestive tract which were filled with these symbiotic microorganisms. Heitz has suggested that the symbiotic bacteria may be able to fix atmospheric nitrogen, and thus solve the protein problem for these cellulose-feeding insects.

The presence of these symbiotic forms extends further than those merely feeding upon wood; for apparently large numbers of insects which feed upon plant tissues which are low in nitrogen and difficult to digest, have the microorganisms always with them. Escherich (1900) describes the internal symbiont from the beetle, *Anobium paniceum*, a beetle which has often been considered as exceptional in its ability to digest cellulose. Ecologically, we may then regard the cellulose of wood as the environmental medium upon which a fauna of microorganisms lives and maintains the insects which normally are associated with the wood. If we were to define an individual organism as one which was capable of inde-

pendent existence, we could hardly call some of these forms organisms at all as they are incapable of living without their symbiotic forms. The unit which is capable of maintaining itself consists of the insect with its great fauna and flora, which it is obliged to have with it always.

The insects which live in the reproductive portion of the plant, which is the seed, utilize a portion of the plant in which food materials are stored for the development of the young plant embryo. They live in a medium which is nutritious and which is ordinarily relatively free from microorganisms. Among this group of organisms we might expect to find

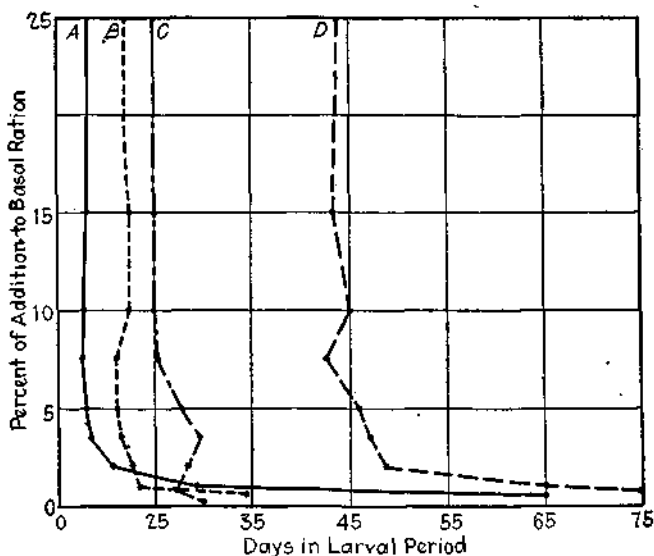


FIG. 57.—Growth of *Tribolium* when a source of Vitamin B is added to a purified basal ration in varying proportions. Addition to basal ration: A, wheat embryo; B, alcoholic extract equivalent to wheat embryo; C, yeast; D, alcoholic extract equivalent to yeast. Basal ration: casein 28, Osborne-Mendel salts 4, ether extract of wheat embryo 3, dextri 65. (From Sweetman and Palmer, 1928.)

insects which were unaided by symbiotic microorganisms. Portier (1919) states that he has been able to rear *Tenebrio* under sterile conditions.

Chapman (1924) reared *Tribolium confusum* on various media and concluded that microorganisms did not play an important rôle. It was found that the slowest growth of the flour beetles took place on flour made from polished rice which might be assumed to contain the smallest amount of vitamine. When synthetic media were used, it was found that the wheat embryo itself gave the greatest acceleration of growth. Sweetman and Palmer (1928) made a critical study of the vitamin requirements of the confused flour beetle, *Tribolium confusum*. Synthetic media were made up which consisted of a basal ration: casein 28 per cent; salts, 4 per cent; fats, 10 per cent; and dextrine to bring it up to 100. To this various other materials were added. Figure 57 shows

the result, when (A) wheat embryo was added; (B) alcoholic extract equivalent to the wheat embryo; (C) yeast; (D) alcoholic extract of yeast. It is interesting to note the sensitivity of these organisms to the addition of some materials. One-half of 1 per cent of wheat embryo, added to the basal ration, shortened the time of development from 65 days on one-half of 1 per cent to 28 days on 1 per cent. When $3\frac{1}{2}$ per cent had been added, the maximum shortening on the life of larvae was found. Beyond this, up to 25 per cent, there is no change whatever. It is also interesting to note that the larvae are just as sensitive to the addition of the alcoholic extract to the wheat embryo; but even when a maximum shortening of the larval period has been attained, it is still longer than it is with the wheat embryo. This seems to indicate that there is a difference between the Vitamine B content of the extract and the wheat embryo itself.

The addition of yeast, likewise, gives a very abrupt shortening to the life cycle; but, again, the shortest life cycle with the yeast is longer than that with the alcoholic extract of wheat embryo or the wheat embryo itself. Still more striking is the effect of the alcoholic extract of the yeast. The shortest life cycle with this is about 45 days as compared with less than 20 days with the wheat embryo.

Other experiments with various parts of the wheat kernel and with corn seem to indicate that the wheat embryo which is notable for its content of the Vitamine B is necessary for the development of the insect; and that when extracts of this, which are known to contain the Vitamine B are added to a ration which is lacking in Vitamine B, the development is greatly accelerated. This evidence seems to make it clear that these insects require the Vitamine B. Apparently when it is present they can develop normally in the absence of microorganisms.

The insects which live in fruits have not been studied extensively from the standpoint of nutrition. However, Buchner (1928) has shown that many of the flies which live in fruits carry microorganisms with them; and the presumption is that they may feed partly upon the fruit and partly upon the microorganisms. The nectar of flowers is an attractive food for a large number of insects. Its presence is explained teleologically as an attraction for insects to insure the pollination of the flowers. The honey bee has received more attention from a nutritional standpoint than any of the other insects depending upon nectar. The work of Phillips (1927) and Bertholf (1927) indicates that the adult bees can maintain themselves by the use of pure carbohydrate; but for the rearing of larvae, nitrogen is required which is obtained from the pollen. These pollen grains are passed through the intestinal tract without any alteration unless they are mechanically broken. This is done by the nurse bees preparing the food for the larvae. Many of the butterflies are able to

maintain themselves in the adult stage with only the carbohydrates which they obtain from nectar. At least some adult butterflies never feed at all, developing their eggs upon reserves of material which have been stored up during the larval stage. We may thus conclude that in the case of phytophagous insects, some of them are highly specialized as they have types of enzymes which make it possible for them to use certain highly specialized foods. Others associate themselves with microorganisms and thereby make it possible to exist on almost pure cellulose.

We shall next turn our attention to saprophagous insects. These are usually defined as those feeding upon decaying and fermenting matter. It is evident at the start, that these insects live in media which may be teeming with microorganisms. The evidence before us at the present time seems to indicate that in general these insects feed eventually upon microorganisms, and that the decaying material is the medium upon which the microorganisms live. The work of Guyénot (1913 to 1917), Delcourt and Guyénot (1910 and 1911), Portier (1911), and others seems, to substantiate this. Baumberger in 1919 has given an excellent summary of the work upon these insects and has performed critical experiments with *Drosophila*. This shows that flesh flies, fruit flies, and many others are unable to live on the sterilized medium. It has ordinarily been considered that the banana is the normal food of *Drosophila*. Baumberger, however, demonstrated that the larvae would die after 28 days on sterile banana; while those fed upon yeast completed their life cycles and pupated after five days (Fig. 58).

It was also demonstrated that if larvae were put on sterile banana for a period of 20 to 25 days and at that time yeast was introduced, larvae proceeded to develop in a perfectly normal way.

When media were made up consisting of various percentages of yeast, it was found that the rate of growth was proportional to the percentage of yeast (Fig 59). The greatest size was attained in a medium containing 24 per cent of yeast. As the percentage of yeast was reduced, the ultimate size of the larvae was reduced; and the time required for them to attain maturity was increased. Number 6 was reared on a medium

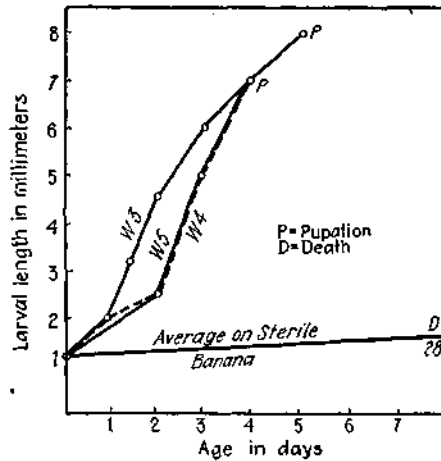


FIG. 58.—Larval growth of *Drosophila* on dead yeast. W 3, 4, and 5 show rapid growth on dead yeast; A shows slow growth on sterile banana. (Baumberger, 1919.)

containing yeast nucleoprotein, sugars, and salts. This seems to show that the proteins of the yeast are adequate to support *Drosophila*. Number 8 was reared on a concentrated extract of banana. This was sterile and seems to indicate that concentrated banana may support growth; but the period was about six times as long as on the yeast food. A less concentrated extract of banana was unsuccessful in bringing about pupation; as was also a 1 per cent yeast culture.

It seems that the action of the yeast may be at least partly quantitative, for a concentrated extract of banana can support *Drosophila*. It may, however, be at least in part qualitative through the synthesizing of certain proteins; for the larvae grew more rapidly and to greater size on a medium which contained the nucleoprotein than on the concentrated banana.

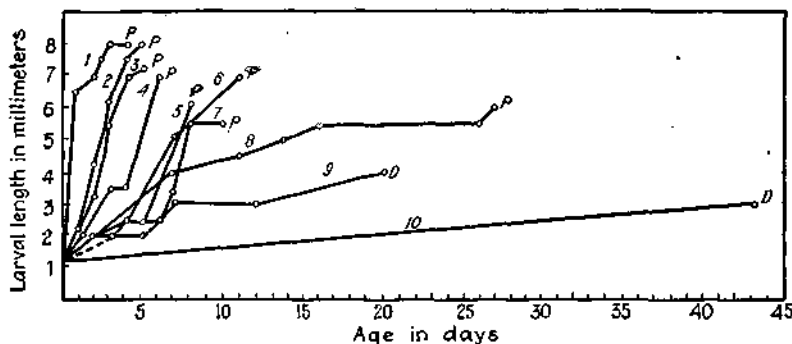


FIG. 59.—Larval growth of *Drosophila* on various media: 1, 24 per cent yeast; 2, maximum 3 to 12 per cent yeast; 3, minimum 3 to 12 per cent yeast; 4, vinegar plant; 5, mushroom; 6, yeast nucleoprotein, sugars, and salts; 7, 2 per cent yeast; 8, hot aqueous extract of banana; 9, 1 per cent yeast; 10, cold aqueous extract of banana. (Baumberger, 1919.)

The larvae of *Drosophila* are able to live upon sterile dead yeast which indicates that there is no requirement of living microorganisms. The larvae of Cecidomyid flies living in decaying bark have also been shown to require microorganisms for their food. We may conclude, therefore, that our term, saprophagous, as applied to the insects which we think of as feeding upon decaying plant matter, is misleading in that these actually feed upon the microorganisms; and that the decaying material is merely the stratum on which the fauna of microorganisms exists.

Turning our attention to those forms which feed upon decaying animal matter, we find a situation quite similar to that with those feeding upon decaying plant matter. Guyénot (1906), Bogdanow (1906), and Baumberger (1919) considered that the food of these insects is essentially the same as that of decaying plant matter, *i.e.*, that they feed upon microorganisms. Wollman (1911, 1919, and 1922) contends that he has been able to rear the larvae of the flesh fly under sterile conditions

and that they were normal in every way. This seems to indicate that there may be some question as to the absolute requirement of the microorganisms. However, the general proposition seems to be quite clear that this is a group of insects which feed upon a medium which is normally teeming with microorganisms.

We shall next turn our attention to the group which feeds upon the excreta of other animals and which is normally termed "coprophagous." From the evidence which has just been put before us we are at once inclined to feel that these insects may also be feeding upon microorganisms. Critical evidence is lacking in nearly all the cases, and a great deal of research is required in this field. Vaternahn (1924) concluded that microorganisms did not play an important rôle in the nutrition of the dung beetle, *Geotrupes*. However, the excreta of the various organisms vary so much in content and nature that it is quite possible that in some cases microorganisms may play no part at all, and that in other cases they may be very important factors.

Under the heading of carnivorous insects, we might include from the viewpoint of nutrition all those forms which live upon other animals in a living state. Ordinarily we speak of carnivorous forms as those which feed upon organisms smaller than themselves; but from the standpoint of nutrition, there can be little distinction between those which are parasites on other living animals and those which feed directly on smaller animals. Among these insects we seem to find all the categories of food restriction that we find in connection with phytophagous insects. Some of these forms are restricted to a single species and, in the case of parasites, the single organs of single species. Others are nearly omnivorous and range widely in their food habits. It is difficult to make many broad generalizations until more critical physiological work has been done upon the nutrition of these forms. In certain cases, at least, these forms may depend upon symbionts for the digestion of their food. Roubaud (1919) made a study of the tsetse-fly; and it seems in this case that symbionts may be necessary for the digestion of the blood which forms its food.

The large range of food habits of insects from those which are intestinal parasites, to those which are wide-ranging carnivores feeding upon large numbers of minute insects every day, presents a big field for investigation; and we must reserve our broad conclusions until more evidence has been presented. We have a host of insects which feed upon special substances, and these have given rise to many rumors with regard to the peculiar digestive powers of insects. The clothes moth, *Tineola ciselliella*, feeds upon a wide range of organic substances, principally hair. Titschak (1922) has made a very careful study of this insect and has shown that the larvae prefer keratin. Feeding experiments with wool proved that keratin undergoes fermentive digestion. By

analysis of the excreta he was able to show that a large portion of it was digested keratin. Albuminoids and carbohydrates were absorbed and other parts were excreted.

The larva of the wax moth, *Galleria melonella*, has been investigated by Sieber and Metalnikov (1904), who showed that the larvae fed not alone upon wax but also upon material containing nitrogenous substances which was found upon the wax in the beehive. It was also demonstrated that they did not grow normally without wax and that much of the wax in the food was digested. It seems that microorganisms are not required in this case, the nitrogen being made up from the molted skins of the bee larvae and other products which are associated with the wax in beehives, the normal environment of this moth. The museum beetle, *Anthrenus museorum*, is known to feed upon a large variety of substances including the dead bodies of insects. Wodsdalek (1917) in a series of interesting experiments demonstrated that it was able to live upon a diet of pure silk in the absence of fats and carbohydrates. The possibility of microorganisms, however, was not excluded.

Special foods are prepared by many of the social insects, particularly for the feeding of their larvae. This is true of the honey bee, the termites, ants, and many other social insects. In the case of the honey bee, a so-called "royal jelly" is prepared by the workers from predigested pollen. This is fed to all the larvae during the early part of their development, but is fed to the larvae which are destined to be queens throughout their whole development. They are able to differentiate their larvae into those which will be workers and those which will be reproductive forms or queens by controlling the nitrogenous contents of the food. Bertholf (1927) and others have made interesting investigations into the physiology of the nutrition of bees. The case of the termites has already been referred to in connection with the work of Cleveland (1923 and 1925). The nutritional specialization of ants is extremely interesting. They prepare special foods; they cultivate fungi, and in general exert a controlling and selecting activity in connection with their nutrition.

Our general conclusion, with regard to the nutritional requirements of insects for the maintenance of metabolism, may be that they have very much the same physiological limitations as other animals have. Ecologically, however, they have been able to exempt themselves from some of the physiological restrictions. First, by associating themselves with microorganisms which aid in the digestion of substances and make available nitrogen under conditions where other organisms would not be able even to exist. Secondly, the social organisms exercise a selection and combine certain food substances making nutrition of their larval forms possible under conditions where other organisms would not be able to exist. Thirdly, through the specialization of the larval stage for nutrition and growth, certain insects are able to exempt themselves from a food requirement during their brief adult stage. This is true of

certain May flies, Lepidoptera, and others. This great ability of insects to adapt themselves to extreme conditions of nutrition is undoubtedly at least partly responsible for their great success on the earth.

Effect of Nutrition upon the Morphology of Insects.—The specialization in the case of insects requiring the larvae to perform the function of growth makes possible a great adaptation to environmental conditions. Many insects are able to adapt themselves to a small food supply by developing small individuals. Hunter and Pierce (1912) found that the cotton boll weevil developed into small adults when the larvae were developed in small cotton squares. Likewise, the bean weevil has been

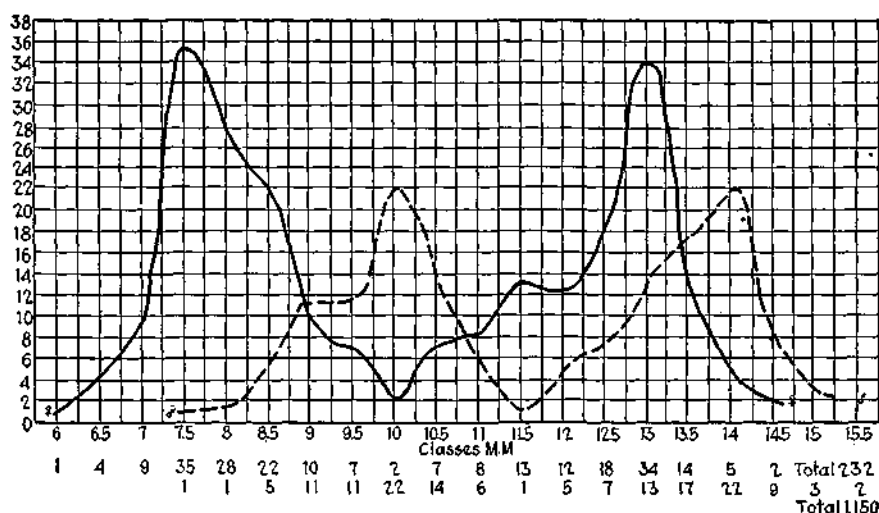


FIG. 60.—Frequency curve of variation in size of male and female of *Dasymutilla bioculata* Cresson. (Mickel, 1924.)

observed by the author to develop into adults of about 8 per cent of the size of the normal adult when they were confined to a small portion of a bean. This regulatory action with respect to size is not well understood. Under experimental conditions it was not possible to remove larvae when they had attained a size equal to that at which others were pupating, and leave them entirely without food, and have them transform successfully. There seems to be some regulatory action for the restriction of food supply.

Mickel (1924) found that a species of *Dasymutilla* which are parasitic upon *Bembix* and *Microbembix*, two genera of wasps, attained a size which is in proportion to the host. Those individuals which parasitized the larger *Bembix* developed into a large mutillids. Those which parasitized the small *Microbembix* developed into smaller mutillids. This accounted for the distribution of size among these mutillids which was found to have a bimodal distribution as shown in Fig. 60. It will

be noticed that the variation in size is almost discontinuous. This might be expected, understanding that the large hosts produce the large individuals, and the small hosts the small individuals which are otherwise identical (Fig 61). Herms (1907) found that the flesh fly, *Lucilia caesar* attained a size which was directly proportional to the number of feeding

hours. The larvae at the end of their period, the weight of the pupae, and the weight of the adults were all directly proportional to the feeding time as is shown in Table XI.

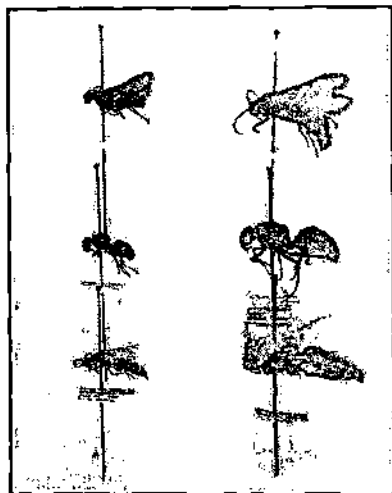


FIG. 61.—Correlation in size between *Dasyneutilla bioculata* Cresson and its hosts *Microbembex monodonta* Say (left) and *Bembix pruinosa* Fox (right). In each vertical row: male above, female in the middle, host below. (Mickel, 1924.)

is probably of great value to these beetles which live on dried bits of skin and bone, and may at times be called upon to endure long periods of starvation.

TABLE XI.—LARVAE OF SARCOPHAGIDAE WERE REMOVED FROM FISH FLESH AFTER DIFFERENT PERIODS OF FEEDING. THE RESULTING LARVAE, PUPAE AND ADULTS ARE TABULATED ON THE BASIS OF AVERAGE WEIGHT,³ (Herms, 1907)

Feeding period, hours	Weight, larvae at end of period	Weight, pupae	Weight, adults
60-72	38.183	30.283	22.283
60	35.68	24.76	18.44
54	31.06	22.38	17.54
48	22.14	11.81	8.08
42	17.06	12.38
36	8.82	9.34	7.15

It is apparently not always true that size is directly proportional to food supply. Chapman (1918) showed that in the case of a confused flour beetle the larvae might attain a large size without being able to transform in foods which were apparently lacking in some essential substance which has to do with the transformation of the pupal stage. Our knowledge of the physiology of control of size in insects is so limited at the present time that we are not warranted in drawing conclusions. It will be sufficient to point out cases cited which are known as the effects of the food and the environment on the size of the insect.

Effect upon the Color of Insect.—From our present knowledge of the pigments which are involved in animals, it seems that they are derived from plant sources already synthesized. A case was investigated by Knight (1924) in which he found that carotinoid pigment of the bug *Perillus* was obtained from its prey, the potato beetle, which in its turn got the pigment from the plant. Toumanoff fed *Dixippus morosus* on carrots and upon white turnips. Those fed upon the carrots showed a yellow color due to the carotinoid pigment. Those fed upon the white turnips showed no yellow color. It is probably well to be conservative in drawing conclusions from the data which are before us as there are metallic colors in insects and also colors which may possibly be synthesized in some other way.

Harrison and Garrett (1926) state that they were able to induce melanism in Lepidoptera by placing twigs of the food plant in a solution of lead nitrate (one grain per liter) before they were fed to the moths, *Selenia bilunaria*. The authors state that these moths have never been taken as normal melanic forms in the wild state, but that they developed melanic forms under the food conditions described, and that a small percentage of this and other species transmitted the melanic character to their progeny. This case raises the perplexing question of the inheritance of an acquired character and therefore may be placed in a debatable class. However, the fact that the pigment of the food plant was incorporated into the insect is nothing surprising and is entirely in accord with our other information.

For the further summary of the physiology of pigments of insects, the student is referred to Uvarov (1928).

The Effect of Nutrition on the Behavior of Insects.—Throughout the class *Insecta*, we apparently have a wide variation in the development of the olfactory senses. Certain insects seem highly sensitive especially to their natural food while others appear to exert very little selective action. Hewitt (1917) summarizes many cases in which it has been possible to attract insects by the use of extracts of their normal food. Minnich (1922) has shown that *Vanessa* is able to detect sugar in a dilution of only one gram-molecular. Richardson (1916) showed that houseflies have some discrimination between nutritious and

non-nutritious substances. On the other hand, the confused flour beetle, *Tribolium confusum*, seems to exhibit relatively little olfactory selection. In case of some insects, the selection is exercised by the stage which does the feeding. In others, the female does the selecting; she deposits her eggs and the larvae hatch surrounded by their natural food. In the latter case, there may be a great conservation of the larvae; for when larvae must shift for themselves in seeking their food, large numbers of them are lost without finding a favorable food plant.

Effects of Nutrition on the Geographic Distribution of Insects.—The experimental evidence which is now at hand relative to the food requirements of insects, makes it evident that each insect has certain minimum nutritional requirements for the completion of its life history. It is obvious that any area which is lacking in any one of these required food constituents for any given species will not have that species present in its fauna. An insect which is limited to a single-host plant will of necessity be limited at least to the area of this host plant.

It is even possible that host plants may be able to tolerate deficiencies in certain salts in the soils of certain areas, but that the insects which normally feed upon them may be unable to use the foliage when it is deficient in this particular salt. Such speculation is, of course, without foundation and is of use only as a suggestion for future investigations.

In concluding this chapter on nutrition, it is realized that the usual lists of host plants have been omitted and that no classification of food habits has been given. It has seemed inadvisable, in our present state of knowledge, to go further than to describe the various parts of plants and animals on which insects normally live. When it has been made certain in which cases microorganisms are the essential food and in which cases the substratum is the only food, if there are such cases, we may then proceed to classify food habits on an intelligent basis.

Our chief conclusion may be that, at the end of our consideration of the physical factors of the environment, we are confronted with the fact that insects are unable to use nutrient materials without some materials which have been synthesized by other organisms.

The subject matter of nutrition furnishes us with an excellent example of the inter-relationship of physical and biotic factors, and of physiological and ecological subject matter. We may logically conclude that nutrition is a biotic factor of the environment, inasmuch as none of these animals are able to live without the use of some material which has been synthesized by another organism. We find also that the nutrition of many of the insects is largely an ecological problem in that these insects have associated themselves with symbionts which exempt them from certain physiological requirements of their own class; or that they have formed social organizations in which certain individuals are specialized for performing the function of preparing food for the others. This vast

subject will merit the preparation of a critical volume presenting the information which has been prepared from various sources of investigation. For further consideration, the student is referred to the paper of Uvarov, and to various other papers listed in the bibliography, which will lead him to the original results of investigations.

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CHAPTER VIII

BIOTIC FACTORS IN AUTECOLOGY

The preceding discussion of physical autecology has followed the usual lines of physiological investigations. Attention is now turned to the biotic factors which are the ones more usually associated with ecological studies. Naturalists have always been attracted by the biotic factors which have not lent themselves so readily to the quantitative treatment used in connection with physical autecology. An attempt will be made to treat the subject of biotic autecology, so far as is possible, in the same quantitative way as was used in the subject of physical autecology. In so doing there is no implication that qualitative observations of biotic factors are not of value; for, in fact, they represent the very foundation upon which all quantitative work must rest.

The primary object of this quantitative attempt in the treatment of biotic autecology is to bring together the widely divergent results of physical autecology of the physiological type, and the biotic autecology of the naturalist. The results in these two fields have proceeded quite independently of each other with a great gulf fixed between them. We have had, on the one hand, a school of ecologists who have been essentially physiological, who have been concerned with temperature coefficients and responses to various physical features of the environment. On the other hand, we have had a school of naturalistic ecologists who have propounded the sound doctrines, that the necessity for food, shelter from the physical factors of the environment, and protection from natural enemies were the most important dynamic factors of nature so far as the survival of the individual was concerned; and that reproduction and distribution were the most dynamic factors so far as the welfare of the species was concerned. This school of natural history has been inclined to feel that the general physical factors operating in the universe were fixed and omnipresent, and were of relatively little concern as compared with the organism's ability to survive against them; and that the chief concern of the ecologists was the study of the ways and means through which the organism was able to maintain itself.

Physical barriers have been considered of relatively little importance because every species has some way to get around each physical barrier. It seems that if progress is to be made in the field of ecology, both of these two attitudes must be brought together and made use of. In accordance with the laws of nature, if two things of divergent character are to be brought together, they must be placed over a common denomi-

nator; and it would seem that that common denominator would have to be a quantitative expression of mathematical nature. Fourier says of mathematics,

It seems to be a faculty of the human mind destined to supplement the shortness of life and the imperfection of the senses; and what is still more remarkable, it follows the same course in the study of all phenomena; it interprets them by the same language, as if to attest the unity and simplicity of the plan of the universe, and to make still more evident that unchangeable order which presides over all nature.

In the field of physical autecology, it has been pointed out that the technique of the physiologists may be followed, and that the limitations of our knowledge are due not so much to the unsurmountable difficulties of technique, as to the lack of data and crucial experiments to demonstrate the fundamental effects of the various factors. In the field of quantitative biotic autecology, there is not only a lack of quantitative data with regard to the fundamental effects of the biotic factors, but there also exist unsolved technical difficulties in the way of accumulating such data and expressing them quantitatively. The transition from physical to biotic autecology might be likened to the transition from arithmetic to calculus and trigonometry. It is necessary to superimpose upon the quantitative effects of physical factors a quantitative expression of all the complicated biotic functions and characteristics. On a quantitative basis, biotic autecology should be destined to develop into one of the highest branches of science. It is not to be denied that there are many difficulties in the way, nor that the relationships to be dealt with are extremely complicated. If this were not true, the future development of this field would be circumscribed. At the present stage of development, the pathway of progress through this field is ill-defined and insecure. Its chief attribute seems to be that it promises to lead to a goal of importance.

Biotic Characteristics of Species.—It is necessary to know something of the biotic characteristics of the organisms which appear as factors in the environment before considering the organism as a factor. It has already been pointed out (Chapman, 1928), that organisms themselves have certain innate biotic characteristics which are at least analogous to the characteristics of physical compounds. These characteristics have been summed up in the general term "biotic potential." This has been defined as the inherent property of an organism to reproduce and to survive; *i.e.*, to increase in numbers. It is a sort of algebraic sum of the number of young produced at each reproduction, the number of reproductions in a given period of time, the sex ratio of the species, and their general ability to survive under given physical conditions. It is the potential power that an organism has to reproduce and survive in its environment.

The Significance of Biotic Potential.—The biotic potential of the species is a quantitative expression of the dynamic power of the species which is pitted against the resistance of the environment in which it lives in its struggle for existence. Organisms which encounter a great resistance from the environment must have a high biotic potential in order that there may be survivors to replace required organisms. Nature has required that organisms which live in environments that offer great resistance, possess a high biotic potential in order that, after all the resistance of nature has been met, there may still be survivors to maintain the population. In the event that the biotic potential was high with reference to the resistance of the environment, the population of the species would increase until it became out of all proportion to the rest of nature. If the biotic potential was relatively low, as compared with the resistance of the environment the numbers of the species would gradually be reduced until it became extinct. The fact that our present fauna has survived down through the ages is evidence that biotic potential and environmental resistance have tended to maintain a balance, just as the various types of physical pressure tend to maintain a balance. Parasitic forms whose life cycles expose them to various hazards of the environment are classically known to have large numbers of eggs produced. Those organisms which live in relatively constant and secure environments produce very few young at each reproduction. Those organisms which have a high biotic potential are able to increase their numbers very rapidly at any decrease in the resistance of the environment. The history of economic biology contains the records of many biotic explosions in nature where there has been a sudden change in environmental resistance; and the biotic potential of the organism has been fully expressed; and populations have shot up to enormous proportions.

Biotic potential is just as definite a characteristic of a species as is the valence of carbon a characteristic of that element. Our common fruit fly *Drosophila*, for instance, is very distinctly characterized by its ability to reproduce rapidly; and its usefulness in genetical experiments has been due to this biotic characteristic. It is obvious that a species like the 17-year cicada, while it might have contained better genetic characters than *Drosophila* would be much less useful in genetical experiments because of the difference in biotic potential. One can pass through a generation in a few days' time; the other requires years of time.

Quantitative work in ecology will require a knowledge of the biotic potential of the species, just as quantitative work in chemistry requires a knowledge of the valence of elements which go into compounds. The reaction of an element may be predicted on the basis of its valence; and the reaction of a species in an environment may be predicted on the basis of its biotic potential, provided the characteristics of its biotic potential are fully understood. It would seem that the general situation of the

biotic potential as an inherent characteristic of the organism on the one hand, and the resistance of the environment on the other hand, should be rather clear. The species is continually reproducing. In this respect it is sometimes very extravagant of individuals; while the environment is continually taking an enormous toll from its numbers. The result is that the population remains relatively constant because such great numbers are produced. Further examples are to be given in the subsequent discussion. For the present, the main object is to make clear the general picture.

It may add to the appreciation of this general situation with respect to the biotic potential of the organism and the resistance of the environment, if we cite a few examples from literature illustrating the capacities of organisms to reproduce. Huxley (1858) cited an example which has become almost a classic in biological literature, showing that a single parthenogenetic female aphid could give rise in a year's time to a population of progeny whose total protoplasm would be equal to that represented by the inhabitants of the Chinese empire. Herrick (1926) tested this calculation using the common cabbage aphid, *Brevicoryne brassicae*, which he had shown to be capable of producing twelve generations between March 31 and Aug. 15. A single stem mother could give rise on an average to 41 young. On this basis, the progeny, if they all lived, would number 564,087,257,509,154,652. He determined the average weight of four aphids as 1.4 mg. Therefore, this number of aphids would weigh 1,645,254,501,068 lb., which seems to substantiate the statement of Huxley.

Woodruff (1922) calculated that it was possible for a single infusorian to produce a cubic meter of protoplasm in 60 days' time with 1,000 individuals to the cubic millimeter. In 7 years' time, the progeny of this single infusorian would be represented by a mass of protoplasm 10,000 times greater than the mass of the earth itself, and that in a few hundred years it would exceed the whole visible universe including the sun and all of its planets.

Lefroy (1909) calculated that a single pair of fruit flies, *Drosophila*, would in one year's time produce 30 broods; and if each brood consisted of 40 eggs, half females; and if all came to maturity, their numbers would be appalling. He said:

If they were packed tightly together so that each cubic inch of space contained a thousand of them, they would very easily cover the whole of India, from Kashmir to Cape Comorin, from Karachi to Calcutta, with a solid cake of flies a hundred million miles thick, or would coat the whole world with a layer of insects a million miles in depth. And yet as it is we do not particularly notice them.

It would be possible to continue to cite similar incidents based upon general observations and general citations in literature. Such calcula-

tions usually are not taken seriously. They are considered to represent fantastic numbers. It is perfectly obvious that these potential numbers are never realized because the various actions of the environment inhibit the reproduction. However, it is just as obvious that they are true potential numbers.

A species without the ability to reproduce rapidly could not produce a large population in a short period of time. The history of economic biology gives the examples of numerous species which have been moved accidentally from one environment to another and in the new environment the population level has been entirely different from that in the natural environment, due to the difference in resistance in the two environments. Tropical species go north until the resistance of the environment overcomes their biotic potentials. Species from the lowlands move up the mountains until their biotic potential is overcome by the environmental resistance.

This general picture does not solve problems, but it may aid in clear thinking as to the relationship of organisms to their environment. To be of use in research in analyzing complicated situations it is necessary to proceed further and analyze more minutely the constitution of biotic potential. It is interesting to note that there are hardly any economic species in which the data are available to determine their potential rate of reproduction. With the hundreds of volumes which have been written on various species it seems surprising that so elemental a fact as the potential reproductive rate should have been overlooked. With the limited information now before us it would be disastrous to make dogmatic statements as to the minute details of biotic potential. Inasmuch as the entire value of the conception depends upon the contributions which it can make to research, it is necessary to proceed cautiously and not to adopt dogmatic definitions on the basis of insufficient evidence. It will probably be necessary to continually make revisions, just as in the tables of atomic weights of chemicals it has been necessary to make revisions.

The Constants of Biotic Potential.—It is necessary to give biotic potential a quantitative expression in order that it may be used in measuring the effect of the environment. In giving it such quantitative expression it is of primary importance that the expression be simple, easily understood, and easily standardized. It is also essential that it should not be prematurely dogmatized and made subject to a series of definitions and revisions which lead to controversy and confusion. The conception of biotic potential pitted against environmental resistance leaves the biotic potential as the absolute optimum of the rate of reproduction of the species when there is no environmental resistance. This conception postulates the condition in which any action of the environment will bring about a reduction of the potential number, or the rate of increase of the population. The situation is therefore simplified in one respect,

the measure of environmental resistance will be the reduction of the rate of reproduction below the optimum of potential.

A rather serious difficulty is presented however in the matter of determining this optimum or absolute biotic potential. It involves both the technical difficulties of making the determination, and the assurance that the determination made is the absolute biotic potential, and not some close approximation to it. If the work on the biotic potential of each species must be held up until this difficult determination is made, it will be a serious interference with progress. For this reason there is a practical advantage in introducing the term "partial potential" to represent the biotic potential of a species under a given set of conditions. We may therefore speak of a partial potential of *Tribolium confusum* at 27°C., 75 per cent of relative humidity, and a nutrient medium of pure whole-wheat flour. It may be advantageous to establish a series of partial potentials along the temperature scale, or along the humidity scale, or over a series of nutrient media.

The absolute biotic potential may then remain a hypothetical number of theoretical value just as the absolute zero on the temperature scale of physical chemistry remains a real but hypothetical value of great theoretical importance. Similarly in the study of a field-crop insect, it is possible by a careful field study to make the determination of the partial potential of an insect for a given year under the field conditions of a specified geographic area. The partial potential quoted becomes of value when comparing different areas and different years and in evaluating the effect of the various environmental factors in reducing the partial potential. A careful investigation of the change in population numbers throughout the life cycle compels attention to the facts which it concerns us to know; *i.e.*, the action of the environment in reducing the population numbers.

In accordance with this hypothesis, biotic potential is a constant; and if environmental conditions were to remain constant the population should also be constant. Such conditions have been brought about under certain limited laboratory conditions (Chapman, 1928). In this series of experiments the environmental resistance was ultimately due to the size of the environment which was measured by the number of grams of wheat flour. Environments of various sizes forming a geometric series were used and they varied from 4 g. to 128 g. Populations of newly emerged adult beetles were introduced into each of these environments to provide one beetle to each 2 g. flour. The numbers of eggs, larvae, pupae, and adults were recorded at various times and the flour was changed at each observation to maintain a uniform nutritive value of the environment. Table XI gives the results of the various counts over a period of over 156 days. In Table XII these counts have been reduced to numbers of individuals per gram of flour.

TABLE XI.—TOTAL NUMBER OF INDIVIDUALS IN EACH ENVIRONMENT. *Tribolium confusum* IN WHOLE-WHEAT FLOUR AT 27°C. AND UNIFORM MOISTURE¹

Days	4 Grams			8 Grams			16 Grams			32 Grams			64 Grams			128 Grams		
	Eggs	Larvae	Pupae	Adults	Eggs	Larvae	Pupae	Adults	Eggs	Larvae	Pupae	Adults	Eggs	Larvae	Pupae	Adults	Eggs	Larvae
0	2	8	16	32
15	41	17	0	2	62	71	0	8	263	280	0	16	631	686	0	32	854	1,543
30	44	74	0	2	30	168	0	8	188	509	0	16	369	1,118	2	32	393	2,371
50	42	45	21	31	47	75	51	79	167	383	310	114	332	792	220	639	1,265	1,204
64	64	20	14	59	107	47	12	144	205	78	36	220	497	400	157	842	2,215	541
78	60	10	6	65	114	11	20	144	330	16	39	158	636	67	159	875	2,705	230
101	89	5	1	66	185	30	0	156	390	46	1	174	861	146	1	928	2,672	318
114	125	2	0	66	180	20	7	156	368	21	13	174	846	97	16	904	2,943	218
134	81	0	0	66	257	3	0	159	460	24	1	174	842	32	4	908	3,805	63
156	89	0	0	65	236	2	0	157	544	8	6	173	837	45	7	902	4,097	63

¹ CHAPMAN, ROYAL N., *Ecology*, vol. IX, No. 2, 1928.

TABLE XII.—BEETLES (*Tribolium confusum*) PER GRAM OF FLOUR¹

Days	4 Grams	8 Grams	16 Grams	32 Grams	64 Grams	128 Grams
	0.5	0.5	0.5	0.5	0.5	0.5
15	15	17	20	17	21	19
30	30	25	26	22	24	23
50	35	33	32	35	32	34
64	39	39	34	39	40	37
78	35	41	39	36	37	39
101	40	46	38	44	49	39
141	48	45	36	43	40	40
134	37	50	41	41	48	45
156	38	49	46	44	45	47
171	46	49	46	43	42	40

¹ *Ibid.*

After a period of approximately 100 days, the number of individuals, as expressed in beetles per gram of flour, becomes constant at about 43.97 individuals per gram and fluctuates about this number.

It will be noted that comparing the number of beetles per gram in each of the environments on any one day, and comparing the number of individuals per gram in any one environment over a series of days, from 100 to 150, the fluctuations are of about equal magnitude. This seems to indicate that it makes little difference whether an environment is as small as 4 g. or as large as 128 g. The number of beetles per gram of flour is about constant. Referring back to the table which gives the numbers of the various stages found in each count it will be noted that thousands of eggs may be present every day but that the populations do not change.

A complete analysis of all the resistance which is met by the biotic potential of these beetles is complicated and difficult. It has, however, been shown that the adults and larvae eat the eggs of their own species. There is apparently no selective action in the eating of the eggs, it being merely an accident, whether an adult or a larva encounters an egg while it is eating flour. However, the incidence of these active forms with the eggs and also the pupae is a matter of the concentration of the beetles in the flour. At low concentration, eggs and pupae escape and develop to become adult beetles. When many of them have developed into adult beetles, the concentration is then so high that relatively few eggs or pupae are able to escape; and the population then remains constant. When the resistance of the environment was experimentally reduced by placing the population in a large environment, the numbers increased rapidly, as might be expected from the presence of thousands of eggs.

It has often been postulated that populations reach a limit due to the accumulation of toxic substances in the environment. In this case the medium was renewed according to a schedule and such an accumu-

lation was impossible. It seems, therefore, that the limitation is simply an accumulation of numbers in a limited environment.

Biotic Constants of Potential.—Attention will now be turned to the factors which go to make up biotic potential. Theoretically we may divide biotic potential into *reproductive potential* and *survival potential*; and each of these may be again subdivided. There may be some question as to the practicability of the use of these divisions in making quantitative calculations with our present amount of knowledge; but a discussion of these various factors will at least contribute to the understanding of the significance of biotic potential.

The reproductive potential is a measure of the ability of the organism to produce large numbers. The survival potential is the ability of the organism to maintain the high numbers. It seems to be a general law in nature that if the reproductive potential is high, the survival potential may not be so high and *vice versa*. Many species produce relatively few young but exercise parental care to see that the few produced actually survive. On the other hand, many species produce enormous numbers of young and leave them to take their own chance in nature, which means that the survival potential is not high.

The question of practicability may be raised in considering the relationship between survival potential and environmental resistance. The calculation of environmental resistance as the reduction of the reproductive potential is relatively simple, as compared with introducing another factor to represent survival potential. It is not possible with the present amount of experience to predict what will be the most practical method of handling these conceptions in making calculations. It is certain that various species differ in their ability to endure severe environmental conditions. This means that the same amount of environmental resistance produces different effects upon different species. This may be explained as being due to the difference of the survival potential of the different species. For example, the lowering of temperature acts as an increase of resistance to all species. However, the point on the temperature scale where the different species encounter the absolute minimum temperature, differs just as the freezing points for various chemicals do, although it is true that low temperature approaches the freezing point of all.

It is possible, therefore, to conceive of survival potential as representing the actual position on the temperature scale where a species would experience its optimum and pessimum conditions. This has furnished the basis for the comparison of various species in the same environment. The difference in the reduction of the potential number of organisms of various species by the same environmental resistance would be a measure of the survival potential of these different species. For practical procedure, therefore, the question may be raised as to whether it is more

advantageous to conceive of the environmental resistance as being a unit for any given set of conditions, and its differential action on different species be conceived of as a characteristic of each species, representing a survival potential; or whether it is better to calculate the environmental resistance for each species separately.

It is under these categories of biotic potential that all the facts of natural-history observation come to find a place and to be analyzed quantitatively. All the intricate adaptations, all the protective habits and reactions if they are of significance to the species must contribute, at least some small amount, to the ability of the organism to reproduce and maintain its numbers. When the welfare of a species is viewed in terms of the population it is able to maintain, all these facts should be able to find their place and be evaluated. It seems likely that many controversies over protective coloration, mimicry, and resemblance might find the solution if they were investigated from the viewpoint of their contributions to the maintenance of the population of the species. Thus, this quantitative approach to the subject anticipates a new light on the observations of natural history.

Reproductive Potential.—The reproductive potential of a species may be divided into the factors of the sex ratio of the population; *i.e.*, the number of females which are going to reproduce, and the number of young produced per each female in a unit of time. If reproductive potential is to be used as a constant in making calculations, it is obviously necessary to search for something constant with regard to the number of young produced. There are theoretically two possibilities in this connection. One is the attempt to demonstrate that there is a constant number of primary oocytes for any given species. Such a demonstration involves many technical difficulties, but a knowledge of the subject would be of fundamental importance. The second is to demonstrate a mean value for the number of eggs produced. It is known, however, that the number of eggs produced is constant within certain limits; but in some species at least the variation within these limits is great. The shad, for instance, is said to lay from 30,000 to 100,000 eggs per season, and the carp from two to four million. Among the insects we may also find examples of very wide discrepancy in the number of eggs produced.

Pemberton and Willard (1918) state that the parasites which they studied, often died with eggs left in the oviduct. Parker (1930) found that under laboratory conditions where an attempt was made to maintain the environment as near the optimum as possible, certain grasshoppers laid more eggs than under field conditions. This would seem to indicate that, in certain species at least, the potential number of eggs is never laid under the conditions of nature. It is interesting in this connection to note that Parker found the increased number of eggs in species which are often pests, and that he did not find such an increase in certain other species

which are not of economic importance. This seems to indicate that of the many species of grasshoppers, it is only the few which are of economic importance which have the potential ability to produce a larger number of eggs under optimum conditions:

Among parasitic organisms in general, there are cases cited where enormous numbers of eggs are produced in order to overcome the enormous resistance of the environment which is experienced before the individuals become established in new hosts. Railliet (1895) states that the tapeworm, *Taenia*, will have at least 8,800 eggs in a single proglotus and may discharge as many as 13 or 14 proglotids per day. These are literally spread broadcast in the environment on the chance that a few will come to rest in the proper hosts.

The phenomenon of polyembryony is found among certain of the parasitic insects; and in this case the female places the eggs within the host and thereby practically insures the development of the egg that is so placed. The egg which is placed, then proceeds to produce many individuals instead of just one. This amounts to an increase in the number of young produced and brings about the increase, after the hazard of environmental resistance in passing from one host to another has been overcome.

Many of the social insects have made the matter of reproduction a social affair rather than an individual affair. The case of the honey bees is arranged to have one individual represent the reproductive power of a colony. The individuals of the colony are specialized as to reproduction, care of the young, and the providing of food, so that reproductive potential and survival potential both become social functions rather than individual functions.

The sex ratio becomes an important factor in reproductive potential because it is the rate of increase of the population rather than that of certain individuals which is of ecological importance. The simplest sex ratio of adult insects is an equal number of males and females which may be expressed as a sex ratio of 0.5. In certain cases the females may greatly outnumber the males, and in some of the aphids and other insects there may even be parthenogenesis. In such a case the sex ratio becomes 1.0 so far as the adult insects are concerned. Holdaway (unpublished thesis) found evidence that under certain environmental conditions there may be a change of sex ratio in *Tribolium confusum*.

For the purpose of population studies one may distinguish between the true sex ratio and the effective sex ratio. The former designates the actual percentage of females in the population and is usually applied to the adult population. The effective sex ratio designates the percentage of the total population capable of producing eggs or young. For all purposes of calculation, it is necessary to know the ratio of the number of reproducing females to the entire population. The expression of

Thompson (1922) may be adopted to represent the reproductive potential of a given generation of individuals: $fs = z$. f represents the sex ratio and s the number of young produced at each reproduction. The product of these two values equals z which will be the value for the reproductive potential. The advantage in using the expression lies in the fact that it makes it possible to evaluate any adaptation either for the production of an increased number of young or an increase in the relative number of females. This factor then represents the increase in one reproduction and is the factor by which the population must be multiplied to raise the number to the population value at the end of one reproductive period.

The practicability of the use of these expressions may be greatly increased by adopting the partial biotic potential for any given set of conditions, as has been already suggested. While the number of young produced and the sex ratios may vary, it has been shown in the case of *Tribolium confusum* that under a standard condition of temperature, humidity, and nutrition these numbers are relatively constant. Therefore we may assign a partial potential for *Tribolium confusum* at 27°C., 73 per cent of relative humidity with a standard whole-wheat flour as a nutrient medium, and obtain results which may be duplicated in a series of experiments without wide variation.

Survival Potential.—A survival potential represents the place in the scale of environmental resistance which an organism can endure. We may compare the action of two different environments upon a given species on the basis of environmental resistance. When we wish to compare the effect of an environment on two different species, we may find that the same conditions offer high resistance for one species and low resistance for the other. It represents a sort of buffering ability on the part of the organisms against environmental resistance. It is possible that the chapters on Physical Autecology would have had much greater ecological significance had they been treated in such a way as to represent the survival potential of the various organisms under various conditions of environmental resistance. This has not been done for the reason that the effects of the environmental factors are represented by very well-established physiological results; while the biotic-potential principle is still in the state of a hypothesis. It has, therefore, seemed best to let the physiological facts stand upon their own foundation rather than to involve them with a theory which demands further support.

It is possible to further subdivide survival potential into nutritive potential and protective potential. Nutritive potential represents the ability of the organism to utilize environmental materials for the support of its own metabolism. An organism which has a potential power of synthesizing food materials in a few compounds in the presence of sunlight, carbon dioxide, and water, has an enormous advantage over those organisms which require their food to be already synthesized. The

chapter on Nutrition has called attention to the fact that all animals, at least those above certain protozoa, require that their protein be in the form of amino acids at least, and that their carbohydrates be sugars or starches. This is due to their limited potential powers of synthesis. There is evidence that certain animals and possibly some insects are able to absorb nutrient materials from solutions in the water. Matheson (1929) has suggested that this is possible in the case of mosquito larvae.

Ecologically the nutritive potential of a species may be greatly increased by symbiosis. An organism which lacks the mechanism for synthesizing in its own organs, may acquire another organism which possesses the mechanism and thus makes itself the equivalent of an organism with these powers. A high nutritive potential may therefore be due to fundamental physiological properties, as in the case of certain plants; or it may be due to fundamental ecological relationships in the case of certain termites which are able to live on cellulose by being associated with microorganisms. We thus have an illustration of emergent evolution in the nutrition of organisms which makes it possible for a highly organized insect, which is actually an association of organisms rather than an individual, to have the potential nutritive ability of a microorganism.

Protective Potential.—Reproductive potential and nutritive potential are concerned with the dynamic properties of the organism in bringing other organisms into existence, and in utilizing the raw materials of the environment to build up protoplasm and maintain metabolism. The protective potential of an organism is concerned with the potential ability to protect itself against the dynamic forces of the environment. Individual organisms exhibit adaptations varying all the way from what seems to be pure chance in surviving to the most intricate protective structures and habits. It is impossible to dwell upon these in detail in the present discussion. In a qualitative way the descriptions and generalizations concerning such adaptations form the subject matter of much of our present-day ecology. Undoubtedly the future is going to see these generalizations translated into quantitative terms which will be a measure of the advantages which the species derives from such adaptations. It will undoubtedly be shown that certain species which do not have the high reproductive potential may yet survive in large numbers due to their ability to protect themselves against the organic and inorganic environmental resistance.

Social insects have made the matter of protection a social function rather than an individual function. Special castes have been developed in various of the social insects such as the soldiers among the ants and termites, whose function it is to protect the social organization against the organisms of the external environment. These soldiers are produced to sacrifice themselves for the protection of the colony in general. Social

insects offer some of the most enticing opportunities for study of the quantitative value of protection.

Environmental Resistance.—There is a great practical advantage in being able to consider both the physical and biotic factors of the environment in the same quantitative way and to measure them with the same scale. In the chapters on Physical Autecology, the physical factors were dealt with in a purely physiological way, although it was recognized that the results were not of the greatest ecological value. However, the biotic factors have not been measured in the same physical terms that are used in connection with physical factors. What is more, they are not susceptible to such measurement, at least not to the same degree that the physical factors are. For this reason, a departure must be made in the method of measurement rather than an attempt to evaluate the biotic factors in terms of physical resistance. The biotic potential of the organism will be taken as the standard of measurement. The environment will be represented as resistance to the biotic potential. The difference between the potential number of organisms as indicated by the biotic potential, and the actual number of organisms as observed in the environment, will be the measure of the resistance of the environment. This method of measuring the resistance of the environment suggests an analogy to the methods used by Fourier in measuring the transmission of heat through solids, and by Ohm in measuring the resistance of a system to the transmission of an electric current. In both cases the resistance was measured in terms of the energy which was being dealt with.

Ohm stated that the amount of current which could be measured at any point in a system depended upon two factors: first, the potential amount of current; and second, the amount of resistance which was offered to that current. If the potential was high and the resistance low, the measurable amount of current would be high. If the potential was low and the resistance was high, the observed amount of current would be small. In any event, the only current which could be observed and measured was the amount which was left in the system after the resistance had been satisfied.

There are two important points for the student of ecology in connection with Ohm's generalization. Ohm did not understand the nature of resistance to an electric current when he formulated his statement which is now recognized as a law of physics. Without understanding resistance he did correctly state the relationship between the potential amount of current, the actual amount of current to be observed along the circuit, and the nature of the circuit through which it passed.

The second important point in Ohm's generalization is the fact that it led to the definition of resistance in terms of the resistance offered to an unvarying electric current by a standard-unit circuit which was chosen

arbitrarily. It is known as the "Ohm"; and the actual unit circuit which it represents is of little consequence now that it has been adopted. Its existence as an accepted unit makes possible the measurement of resistance; and by the use of Ohm's law it is possible to calculate the current which will pass through a circuit when the resistance of the circuit and the potential amount of current are known. It is also possible to calculate the resistance of the circuit when the potential amount of current at one end of the circuit and the actual amount at the other end are known.

It is possible to calculate the potential number of individuals that a species will produce if we assign a partial biotic potential to the species as the result of an investigation of its sex ratio and the number of young produced in a unit of time under given conditions. It is also possible to measure the number of individuals which are actually present in the environment at any time. The difference between the two numbers thus obtained must represent the reduction of the potential number of individuals by the resistance of the environment, in much the same way that the resistance of an electric circuit reduces the current from its potential to its actual value.

Since the biotic potential of a species is balanced by the environmental resistance, certain biologists have concluded that it is of no importance because it is always nullified by the resistance of the environment. If the state of equilibrium was absolutely stable this would be true. However, the oscillations of the population are a function of the biotic potential and these oscillations are the important variables. They are perhaps most important in environments in which the physical resistance is subject to wide and extreme fluctuations. In the case of a species which is moved from one environment to another the biotic potential is important in determining the trend of the population of the new species.

The Measurement of Environmental Resistance.—It will not be possible or practical to review the attempts to express the effects of the environment in diminishing the potential number of organisms in an environment. It is still too early in the history of these attempts to be able to select the most promising methods.

Lotka (1925) has devoted considerable attention to the consideration of equations to express the various conditions of equilibrium. In his chapter on "Analysis of the Growth Function," this author uses the terms "birth rate" and "force of mortality" in somewhat the same way that biotic potential and environmental resistance are used here. Lotka presents many ingenious and suggestive formulae for expressing the various conditions of equilibrium which may be found in nature. It is interesting to note the application of these formulae, primarily from the field of physical chemistry, to systems composed of living organisms. The advent of such methods in the field of chemistry led to a great

advance in our knowledge of the structure and energy relationships of chemical systems; and it is possible that they may be a great aid in the understanding of the relationships of systems composed of living organisms.

It is possible that too much stress on analogies drawn from afar may confuse the situation. Proof will not come from the contemplation of analogies unless such contemplation stimulates investigation which results in the accumulation of significant facts.

The statement that the ratio of the actual number of individuals to the potential number of individuals is a measure of the resistance of the environment may serve as a hypothesis. The resistance of the environment consists of many factors which may be classified as physical and biotic. Each of these may in turn be divided into individual factors. For the purpose of a general statement with regard to the measurement of environmental resistance, it will be permissible to treat the total resistance rather than the individual factors, just as Lotka (1925, page 162) has done in a similar computation.

The essential point of the hypothesis presented here is that it proposes the measurement of environmental resistance in terms of the potential number of organisms. By using these three values, biotic potential, the actual number of organisms present in the environment, and the resistance of the environment, we have two values which may be determined by examination. The biotic potential may be determined as previously stated. The actual number of organisms, present in the environment, should be subject to determination. The ratio of the number of organisms which should be present because of the inherent ability of the organisms to reproduce themselves (the biotic potential) and the number which are present may be considered as the measure of the resistance of the environment. If it were not for the environment, the potential number would be reached. In an environment in which all of the factors were at the optimum, the potential number would be realized. In an environment in which the conditions were all near the minimum of toleration, the numbers would depart very far from the potential number of organisms.

Thus when the biotic potential is constant and the number of individuals is high, environmental resistance must be low, and when the number of individuals is low, the environmental resistance must be high.

An example of the relationship of actual numbers of individuals to the potential number may be taken from the results of the bird census taken by the U. S. Biological Survey (Cooke, 1923). There were 11 nesting pairs of English sparrows to each 100 acres of land in the North Central states during the period from 1916 to 1920. The smallest number in any year was nine and the largest 13. It was originally estimated that a single pair of English sparrows would give rise to 275,716,983,698

individuals in 10 years' time (Barrows, 1889). Yet under the conditions in the North Central states, the number has been 11 nesting pairs to each 100 acres of land; and the fluctuation has only been between nine and 13 during this five-year period.

Adopting the rate of increase just cited, each 100 acres of land should have given rise to 575 sparrows each year, but the number remained constant. This difference between the potential number of sparrows and the actual number must be a measure of the toll taken by the environment; or, stated in the terms of the present hypothesis, the resistance of the environment. In the North Eastern states the resistance of the environment seems to be greater; for the average number of nesting pairs was only five; and it varied between three and seven.

The equilibrium of nature is in general a moving equilibrium as cited by Lotka (1925), with fluctuating numbers rather than absolutely constant numbers. If numbers were to be absolutely constant it would be expected that all environmental conditions were also constant, which obviously does not happen in usual cases. Additional examples of such equilibria will be cited under the subject of physical resistance and biotic resistance.

Physical Resistance.—In the chapters on Physical Autecology, the effects of the various factors were considered in much the same way as they would be treated in general physiology. The measurements of the various factors are in terms of physical systems. When considered as environmental resistance, the effect of these factors must be measured in terms of the reduction of the potential number of organisms. This furnishes a good example in making the distinction between physiology and ecology. In the consideration of temperature as a physical factor, the coefficient for the various processes of metabolism in organs or in individual organisms was considered. As pointed out in that chapter, many of these are not of direct ecological importance.

Ecology is concerned with the groups of organisms; and it is the effect of temperature upon the population which is of ecological importance. The effect of temperature upon the rate of hatching of an egg is of indirect importance to ecology, just as the effect of temperature on surface tensions or any other physical phenomena is of fundamental importance to physiology. The interest of ecology is centered upon the trend of the population, just as the interest of the physiologists is centered upon the metabolism which is a summation of all the physical phenomena involved.

Table XIII represents the resistance of temperature to the development of *Tribolium confusum*. It will be noted that the change in the rate of the hatching of the eggs, development of larvae, and the development of pupae, each has its own coefficient. It is also evident that the per cent of mortality changes with temperature. Each contributes to the general rate of increase of population; but it is the algebraic

TABLE XIII.—BIOTIC CONSTANTS FOR *Tribolium confusum*

Stage	17°				22°				27°				32°			
	Time		Per cent		Time		Per cent		Time		Per cent		Time		Per cent	
	Average numbers		Average numbers		Average numbers		Average numbers		Average numbers		Average numbers		Average numbers		Average numbers	
	A.	B.	A.	B.	A.	B.	A.	B.	A.	B.	A.	B.	A.	B.	A.	B.
Eggs.....	38.8	27.5	100	100	14.09	77	100	100	6.04	90.0	100	100	4.41	92.5	100	100
Larvae.....	25	30	60.00	77	78	76	22.42	93.5	88	92	17.35	84.0	93	92
Pupae.....	17.20	80	64	54	8.64	82.0	88	86	5.37	86.0	78	76

sum of these as represented in the rate of population increase that becomes the center of interest for ecology.

The table also gives the history of two series of experiments starting with 100 eggs each. In this case there is an accumulation of time and mortality for the death rate in each stage, as applied to the number of individuals which have survived the former stages. At 22° the percentage of mortality, which represents an unknown resistance factor, is 23 per cent in both the egg stage and in the larval stage; however 23 of the original population died in the egg stage; while the average deaths in the two larval populations was only 17.71.

This is an example of the chain-resistance reaction which is characteristic of organisms with specialized stages in their life cycle. A study of the resistance in one stage does not necessarily give a true value of the resistance to the life cycle. Chains of resistance will be considered further in connection with synecology.

A study of the time, required for the complete stage, shows that the effects of temperature are in essential agreement with the principles of Krogh and Van 't'Hoff as described in the chapter on Temperature. When attention is turned to the population increase during a period of time, it becomes evident that one cannot make an approximation on the basis of temperature coefficients.

Figures 62 and 63 indicate the rates of increase of population at the temperatures indicated, covering the time from the first oviposition of the original population to the beginning of oviposition by the first progeny. It seems obvious that the refinement of the expressions of Q_{10} and various other temperature coefficients is of relatively little direct importance to the ecologist as compared with

the study of the rates of increase of population under various conditions of environmental resistance.

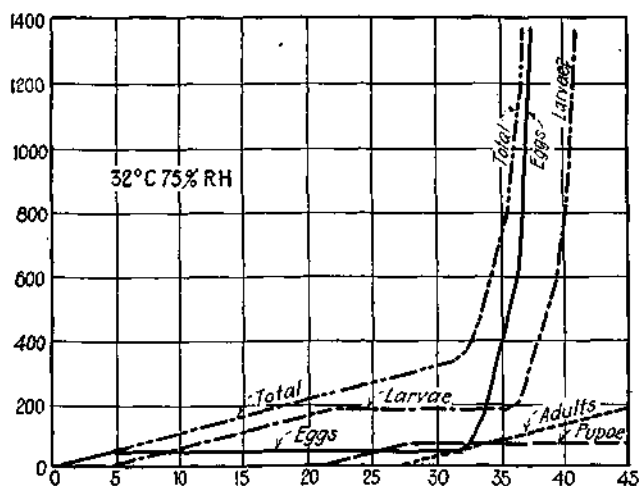


FIG. 62.—Population trends for *Tribolium confusum* from first oviposition of original population to the first oviposition of the first progeny. Number of individuals on the ordinate and days on the abscissa.

In considering the effects of physical resistance and the operation of the total physical and biotic resistance on the life of an individual, it

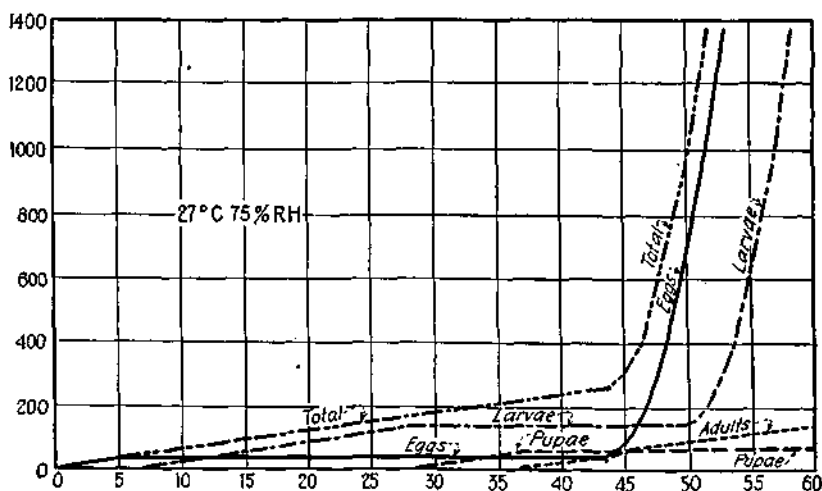


FIG. 63.—Population trends for *Tribolium confusum* from the first oviposition of the original population to the first oviposition of the first progeny (27°C. and 75 per cent of relative humidity). Compare with Fig. 62 for the effect of a difference of 5° in the temperature of the environment.

is necessary to take into consideration the limiting of individual factors which are near the limits of toleration, as the effect of the relative impor-

tance of various other factors operating contemporaneously. Our present knowledge of these total effects is very limited. We are in about the same relative position that general physiology was, when it began to realize the importance of the various phenomena of physical chemistry which contribute to the rates of metabolism.

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CHAPTER IX

SYNECOLOGY

The discussion will be interrupted at this point, only to call attention to the fact that the transition is now being made from autecology to synecology. In autecology individual physical factors and individual organisms were considered. Now individual organisms are to be combined into the populations; and individual physical factors into weather, climate, soil, and other environmental media. In the treatment of the subject matter of autecology, physical factors were given first consideration. In the treatment of synecology the population systems will be given first consideration. Ordinarily the combinations of physical factors which make up weather, which is a study of the variations of these physical factors in time, and the combinations which make up climate, or climatology, representing the distribution of these physical factors over geographic areas, are considered as separate subject matter. In the present consideration there is no separate chapter devoted to weather or to climate. Climatology is considered under chorology or distribution in space, and weather, is considered under both the subject of Chorology and Chronology. It is possible that this division of the subject matter will not be the most satisfactory to students who are particularly interested in weather and climate. However, for those who are interested in the distribution of insects, in space and time, it may prove more convenient.

In considering the populations of animals there are several possible viewpoints. From the viewpoint of biocenology the population, or biocenose, may be classified on the basis of the bond which is of primary importance in holding the population together as an ecological unit. In many cases this bond may be primarily physical, *i.e.*, the organisms may be forced to associate with each other because they have a similar toleration of physical conditions of the environment. In this case the biotic relationships are secondary. These biotic relationships are forced upon the organism as a result of their aggregation on the basis of a physical factor.

In other cases the primary bond may be biotic, *i.e.*, it may be an association of organisms on the basis of some biotic bond such as a social aggregation. Here we could classify the social insects with their parasites and symbionts. Here also could be classified the groups of organisms which have common host plants. It is this phase of ecology that appeals to the naturalist. It represents a serious branch of science with great

possibilities as illustrated by Wheeler's "The Social Insects" (1928). However, in the present volume there will be no special chapters devoted to these subjects. They will be referred to in connection with the populations of various areas and in connection with the chorology involved. Possibly any scheme of handling the subject matter of synecology will prove unsatisfactory to students interested in particular subjects. An attempt will be made to treat it with a dynamic viewpoint with particular reference to methods which may aid in furthering our information of the general subject matter. Under each of the principal headings the main literature will be cited. It is probably true that the student will find more satisfactory information if he will follow these main citations than by using the present treatment alone.

Biotic Potential, Environmental Resistance, and Population Equilibrium.—Biotic systems may be considered as in equilibrium when the populations remain approximately stationary over a considerable period of time. Lotka (1925) prefers to use the term quasi-equilibria for such systems because there is a continual dissipation or degradation of energy involved in maintaining the stationary state. This, he believes, makes a proper distinction from the true equilibrium of physical systems in which all forces are balanced and velocity vanishes.

The relatively stable state of biotic systems resembles the static equilibrium, in that the point or line about which it oscillates is itself stationary. It is, however, like a dynamic system in that the population is moving about a stationary point, but it is nevertheless moving. It is, therefore, necessary to be clear as to the conditions to be considered. A population may be treated, in a general way, as in a stationary state in which its biotic potential is balanced against the environmental resistance.

Individual organisms are continually being produced to replace those which are eliminated by the resistance of the environment. At times the trend of the population is slightly upward, and at times it is slightly downward. This represents the stationary state of equilibrium, or the state of quasi-equilibrium of the oscillating population. On this basis, the general situation of a population may be considered as balanced with its biotic potential equal to the environmental resistance; but the statement does not apply to the population as it follows its oscillation above and below the level which may be called its stationary state.

The economic entomologist becomes impatient to apply a formula for the solution of his problems. However, the present state of our knowledge is too immature for such applications. It is evident that a species of high biotic potential has the ability to increase its population very rapidly if there is a reduction of environmental resistance. Similarly, if the population is reduced artificially, it has the ability to return to the original population in a very short period of time, because of its high biotic potential.

It may be concluded from the above that, when the population remains constant with a low physical resistance, the biotic resistance must be high. Conversely, when the biotic resistance is low, the physical resistance must be high if the same state of equilibrium is to exist. This is in accordance with experience in the biotic control of pests. In countries where physical factors are moderate and relatively constant, pests have often been successfully controlled by parasites and predators; while such control has been difficult in countries where physical conditions fluctuate greatly and often become extreme.

For a consideration of the calculation of the trends of the populations, the student is referred to the Appendix by Dr. Volterra.

Biotic Resistance.—When we approach the subject of biotic resistance, particularly in connection with the equilibrium of populations, we are in the borderground between autecology and synecology. The discussion will be continued from the consideration in the last chapter on Autecology. It is perfectly clear that we are analyzing the effects of organisms upon each other, and this may very logically be the subject matter of synecology.

The history of economic entomology contains the records of many unintentional experiments in which organisms have been carried to new environments which contained no biotic resistance in the way of predators, parasites, or competitors. In many cases the physical resistance has been about the same as in the original environment, but the absence of the biotic resistance has been enough to permit the biotic potential to express itself and the populations to rise to unprecedented numbers. In such cases it has seemed obvious that the most promising method of control is to examine the original environment to determine the nature of the biotic resistance, with a view to introducing it into the new environment and thus reestablish the equilibrium of the original environment.

When the sugar-cane leaf hopper, *Perkinsiella saccharicida*, was introduced into the Hawaiian Islands, it apparently came without biotic resistance in the form of parasites; and the new environment presented a minimum of physical resistance. As a consequence, its rate of reproduction was practically that of the unimpeded biotic potential. Later, parasites were introduced and, in the presence of this biotic resistance, the hoppers were reduced to a minimum which is no longer of economic importance.

Environmental resistance must necessarily be determined for each stage in the life cycle of an organism. Thompson (1928) has called attention to the necessity of properly evaluating resistance factors which function as a part of a chain series of resistances, each operating in a different stage of the life cycle. He calls the mortality of a population as expressed in the per cent of the total individuals in a given stage the "apparent mortality." The real mortality is defined as the per cent

of the egg population of the life cycle which dies. To illustrate the relative importance of apparent and real mortality, he gives a hypothetical illustration of an insect depositing 100 eggs for whose control a 98 per cent mortality is required. The chain of factors are given by Thompson (1928) as follows:

Stage	Factor	Apparent mortality, per cent	Real mortality, per cent
Eggs at deposition.....	Sterility	5.00	5.00
Eggs after deposition.....	Egg parasites	10.00	9.50
Young larvae.....	Intrinsic factors	80.00	68.40
Mature larvae.....	Larval parasites	60.00	10.20
Mature larvae.....	Agricultural factors	30.00	2.05
Pupae.....	Pupal parasites	10.00	0.47
Adults.....	Meteorological factors	54.86	2.30

The fact that a mortality of 54.86 per cent among the adults should make a difference of only 2.3 per cent in the population of the cycle is striking.

Thompson then proceeds to calculate the effect of removing the parasites which caused a 10 per cent mortality among the eggs, a 60 per cent mortality of the larvae and a 10 per cent mortality of the pupae. While the sum of these three amounts to 80 per cent, it makes only a difference of 4 per cent in the total mortality of the cycle. From this he concludes: "The absence of the parasites would allow the escape for reproduction of only two additional females per hundred." It is worthwhile to note that these two extra females would give rise to an extra 200 eggs, making a total of 300 eggs to start the next life cycle instead of the 100 with which he started his calculation.

In many cases the measurement of the total resistance may be of the greatest importance and in certain cases it would be impossible to calculate the total resistance on the basis of any measurement of the resistance to the different stages of the life cycle. Obviously the greatest progress is to be made by combining analytic work in a laboratory where resistance is determined down to the finest point both from the standpoint of the environment and the organism, and observations and measurements in the field where the total conditions are to be met with. When the results of these two types of investigation are in harmony, it may be assumed that the essential facts of the situation are known. When there is a discrepancy between the two types of information, it may be assumed that there is some unknown resistance which has not yet been determined.

Attention may now be turned to the consideration of the various types of biotic resistance which may be encountered in the environment. Attention has been called by some authors to the practical value of various organisms in regulating populations of insects (Forbes, 1883, and others).

This work has had a tendency towards certain more or less quantitative field observations and the formulation of general principles. There has been a tendency towards the production of generalizations with regard to the balance of nature on the one hand, and the attempt at the control of numbers of organisms of economic importance on the other. The general situation in regard to the balance of nature in connection with mammals has recently been emphasized by Grinnell (1928), and has been given a rather full treatment by Elton (1927).

The problem has also received attention from those interested in a more formal mathematical expression. The authors have been both mathematicians and biologists, such as Muir (1914), Thompson (1922 to 1924), Lotka (1925), D'Ancona (1927), Pérès (1927), and Volterra (see Appendix). These authors have been interested primarily in the mathematical theory of population change, and the state of moving equilibria in natural systems. All of these various attempts have, in general, recognized the necessity for accepting a potential rate of increase for a species, and expressing the action of the environmental factors in terms of the change of the trend of population. The biologists have used simple arithmetical formulæ having to do with the number of generations of organisms, while the mathematicians have been inclined to use the compound interest law, or some modification of it, to follow the trend of population.

Mathematically, one of the simplest cases which we have is that of one species which feeds upon another. This may represent the relationships of predator and prey, or of insect parasites and insect hosts. In the case of insects, the distinction is usually made on the basis of whether the predator attacks one host or many hosts; but if it attacks a single host for the support of its entire life cycle, it is usually classed as an insect parasite. Forbes (1883) turned his attention to the action of predators in maintaining the state of equilibrium in nature. He made a comparison of environments in which the numbers of insects were normal, so far as could be determined, and conditions in which there were outbreaks of insects. A study was made of the food which was consumed by birds in these two types of environments (Fig. 64). The accompanying histograms show the general nature of the results, which tend to show that the total

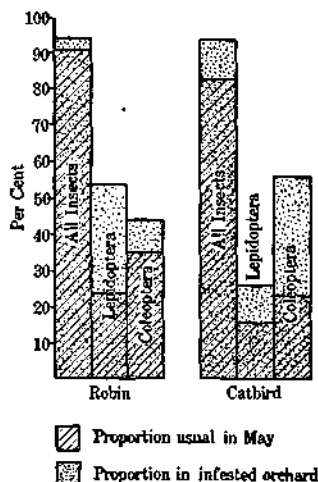


FIG. 64.—The food of birds from an infested orchard compared with the usual food during the month of May. There is a slight increase in the percentage of all insects in the total food and a significant increase in the percentage of Lepidoptera and Coleoptera in the food of the birds from the infested orchard. (Forbes, 1883.)

per cent of insects in the food is higher in orchards in which there were outbreaks of insects than in other environments; and also that the various birds tended to consume more of the abundant species than they did of the others. Forbes considered that this showed that the birds should have a considerable regulatory action in that they would eat the largest numbers of species which were abundant and thus permit species which were low in numbers to increase, while those that were high in numbers would be brought down towards an equilibrium stage. Bryant (1912) made a study of the grasshoppers eaten by birds in areas where there were different grasshoppers populations known to be present. He found that birds ate 120,453 grasshoppers per square mile, when the population of grasshoppers was 20 or 30 per square yard or 635,000,000,000 per square mile. This represents 0.019 per cent of the population eaten by the birds per day.

Muir (1914) considered a theoretical example which postulates a constant number of the total of three species present in an environment, and also a differential action of a predator on the three species so that during the larval stage of species *A* none of the larvae were destroyed; 25 per cent of those of species *B*; and 50 per cent of the larvae of species *C*. In his calculation he maintained the sum total of species *A*, *B*, and *C* as a constant number, and followed the trend of each individual species to show the rate at which species *A* would supplant species *B* and *C*. The following graph illustrates the trend which he found from his calculation (Fig. 65). This is, of course, a case of unstable equilibrium which is tending rapidly to the establishment of one species and the exclusion of others. It may, however, be taken to represent a species which has been introduced into an environment, and has the advantage over two native species in that it is exempt from predators.

Muir (1914) has also represented the case of unstable equilibrium with a parasite and a host. The rates of reproduction are assumed to be the same in both parasite and host; and the assumption is made that each parasite destroys a host and that there is no duplication of parasitism. The accompanying graph follows the trend of the population of the host and parasite, starting with the host free from parasites for the first four generations (Fig. 66). After this the parasite is introduced, and the rate of reproduction in the parasite is the same as that of the host. Seven generations after the parasite is started, it equals the host in numbers; but, nevertheless, the host population tends to increase up to within two generations of the time when it entirely disappears. This is interesting as a case of unstable equilibrium in which the effect on the host is not superficially noticeable up to the time when it is about to be entirely eliminated. It is possible that certain sudden fluctuations in numbers in nature are due to actions of this kind, where the significance of relative numbers of host and parasite are not realized, until the point

is passed in which the parasite equals the number of its host and the sudden change comes about. Such conditions, however, are probably the exception rather than the rule in nature. A more stable equilibrium is undoubtedly the rule.

There is some advantage in following these theoretical considerations of the actions of parasites and hosts if for no other reason than that they can call attention to the relative value of the various factors which must

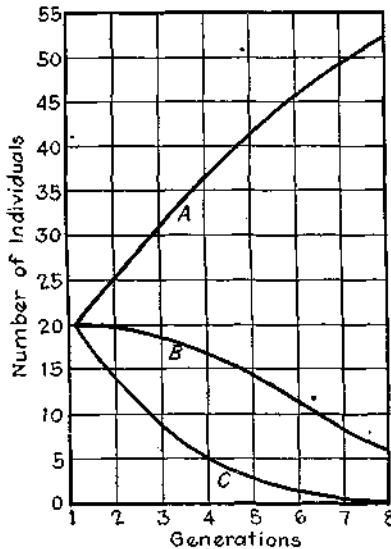


FIG. 65.

FIG. 65.—The theoretical trend of three species whose total population remains constant at 60; 50 per cent of the larvae of species C are destroyed by predators in each generation, 25 per cent of species B, and none of species A. (Adapted from Muir, 1914.)

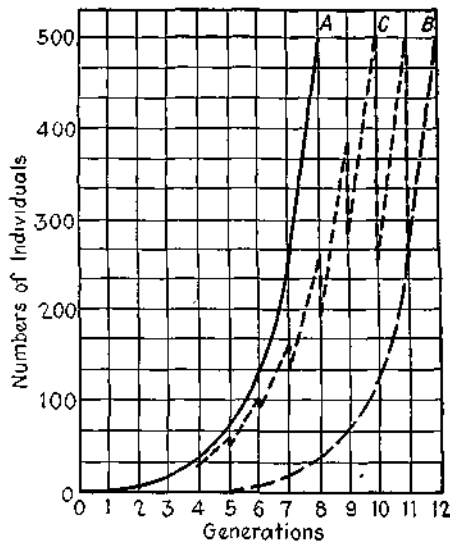


FIG. 66.

FIG. 66.—A hypothetical case of the effect of a parasite on the population of a host. A, host; four young and sexes equal. Population trend without parasites. B, parasite; four young and sexes equal. Each one causes the death of one mature host. C, trend of the host population as a result of the action of the parasites. The parasite starts at the fourth generation of the host and lays four eggs with the result that only 28 out of a possible 32 hosts develop. If this continued the host would become extinct very suddenly in the eleventh generation. (Muir, 1914.)

be involved in the expressions, and thus to an appreciation of the advantages of various adaptations.

Thompson (1922 and 1924) has proposed a formula for the calculation of the number of generations required for the termination of such an unstable state of equilibrium as is indicated above. Such calculations are as yet theoretical, but they have great possibilities.

A slight modification of Thompson's formula for calculating the number of generations required for a parasite to overtake a host is presented. The example is as follows:

- n = the original population of the host.
- l = the sex ratio of the host.

- h = the number of young produced by each female host.
 p = the original population of the parasite,
 f = the sex ratio of the parasite.
 s = the number of young produced by each female parasite.

The calculation may be simplified by combining the sex ratio and the number of young produced as a sort of expression of the biotic potential and thus have one character to handle rather than two.

- $lh = w$ = ratio of reproduction (reproductive potential) of the host.
 $fs = z$ = rate of reproduction (reproductive potential) of the parasite.
 nw = the number of hosts after the first reproduction.

Then

- pz = the number of parasites after the first reproduction.
 $nw - pz$ = the number of surviving hosts after the first generation.
 pz^2 = the number of parasites after the second reproduction.
 $(nw - pz)(w)$ = the number of hosts after the second reproduction.
 $(nw^2 - pzw) - pz^2$ = the number of surviving hosts after the second generation.

To solve for $(nw^k - pz^k) - pz^k$, where k = the number of generations until the population of parasites will equal the number of hosts, the calculation may be simplified and reduced to the following:

$$\begin{aligned}
 O &= \frac{w}{z} \\
 B &= \frac{zp}{n(z - w) + zp} \\
 k &= \frac{\log B}{\log O}
 \end{aligned}$$

In this case it is assumed that there is no duplication in parasitizing the host. It is also assumed that each egg of the parasite is laid in a host and that each host is killed after being so parasitized.

The formula thus represents the increment of difference in the biotic potential of the host and the parasite, and will obviously hold for conditions in which the value for reproductive potential of the parasite is greater than the reproductive potential of the host. If the converse were true, it would be impossible for a time to come when the parasite population would equal the host population. In a case where the two potentials are equal, the increment of difference in the two values for the biotic potential is reduced to zero; and the number of generations required for the host to overtake the parasite may be determined by dividing the host population by the parasite population.

In this simple case we have been able to calculate the value of the parasite as environmental resistance to the biotic potential of the host. It is true that we have made certain assumptions as to the lack of duplication on the part of the parasite, but this and similar factors may be taken care of by determining the per cent of duplication which normally takes place. It also assumes that the host population is continually increasing, which is contrary to the normal condition of equilibrium.

Thompson (1924) has made considerable progress in calculating the value of hazards in the life of the parasite. As stated above, however, the formula as presented does not take care of the case of stable equilibrium between the parasite and host. There is a great practical value even in this calculation. According to Thompson it would require 19 generations for 1,000 individuals of the parasite, *Liparis dispar*, to exterminate 1,000,000,000 hosts when the parasite is reproducing twice as fast as the host. Even under these conditions, 10 per cent or less of the host would be attacked up to the 16th generation. Without a method of calculation, there would be no way of knowing whether the parasite was making satisfactory progress when, after 15 generations the per cent of parasitism was still below 10 per cent.

From our study of insects of economic importance, we now know very well that there are many cases in which the numbers of parasites do not reach a large per cent of those of the host. They seem to come to an equilibrium, when the numbers of the host have not been materially affected. Attention has been called to this by Chamberlin in the case of the alfalfa weevil; and there are many other cases now well known which seem to substantiate the hypothesis that in nature, ordinarily, things come to a state of at least semi-stable equilibrium.

Lotka (1925) illustrates a state of stable equilibrium by the use of the population of the United States and the population of sheep which it uses for part of its food. This example has been chosen because the quantitative data were at hand and it seemed to satisfy the conditions of such an equilibrium. Lotka gave this formal expression in the following way:

$$\frac{X_f}{X_i} = \frac{V_{fi}u_i}{\alpha_{fi}v_f}, \text{ or } X_f = \frac{V_{fi}u_i}{\alpha_{fi}v_f}X_i.$$

The human population which consumes the sheep is represented by $X_i = 103,587,955$ individuals. The population of sheep which serves as food is represented by $X_f = 48,873,000$ individuals. The quantity of sheep eaten by each human individual per year is represented by $V_{fi}u_i = 0.1096$ individual sheep. The per cent of the standing population of sheep slaughtered each year is represented by $\alpha_{fi}v_i = 0.2322$.

The state of equilibrium would, therefore, be represented by:

$$\begin{aligned} X_f &= \frac{0.1096}{0.2322}X_i \\ &= 0.4718X_i \\ X_i &= 103,587,955, \end{aligned}$$

Hence

$$\begin{aligned} X_f &= 0.4718(103,587,955), \\ X_f &= 48,873,000. \end{aligned}$$

The population of the predators is, therefore, multiplied by a coefficient which expresses the ratio of the number of individuals of the prey